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Abstract

Habitat management through increasing plant biodiversity is known to impact insect populations, both herbivores and their natural enemies. Field studies were conducted during 2003 to 2005 at Lacombe and Beaverlodge, AB, Canada to manipulate weed populations in both species of canola, *Brassica rapa* L. and *Brassica napus* L., to investigate responses among root maggots (*Delia* spp.) (Diptera: Anthomyiidae) and selected species of natural enemies.

Delia radicum (L.) is univoltine in canola and peak emergence occurred after approximately 346 degree-days, and 50% flight activity required approximately 325 degree-days (soil base 4.0°C). *Delia platura* (Meigen) is bivoltine in canola and peak emergence of the first and second generations required approximately 340 and 595 degree-days, respectively (soil base 3.9°C). Peak flight activity occurred after approximately 255 and 640 degree-days for the first and second generations, respectively. Peak levels of activity density for the root maggot predator-parasitoid *Aleochara bilineata* Gyllenhal, a staphylinid beetle, required 534, 380, and 559 degree-days and 195, 180, and 186 Julian days, respectively, in each of the three years. *Aleochara bilineata* populations in canola were well synchronized to exploit the pre-imaginal life stages of its principal hosts, *D. radicum* and *D. platura*.

Herbicide rate manipulations enabled establishment of canola with varying densities of weeds. Root maggot damage decreased significantly with increases in monocotyledonous weed dry weights for both canola species at both study sites. The relationship between dicotyledonous weed biomass and root maggot infestations varied among sites, depending on the species of weeds that dominated at each site. As weed

biomass declined the activity density of *A. bilineata* increased. Significant preferences for canola species were found among several important predaceous carabid beetle species and the staphylinid *A. bilineata*.

A diverse fauna of coleopteran predators and parasitoids exists in canola, and my research demonstrated that several species of Carabidae that prey upon root maggot eggs and larvae seem to exhibit species-specific preferences for canola species and level of weedy background. However, the usefulness of utilizing reduced herbicide rates to manipulate weed populations in canola requires some caution in light of the potential development of herbicide-resistant weeds.

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Chapter 1: Introduction

1.1 General Introduction

Root maggots (*Delia* spp.) (Diptera: Anthomyiidae) are serious pests of cruciferous crops (Brassicaceae) in Europe and North America. Larvae of at least three root maggot species are well-documented primary pests, including *Delia radicum* (L.), *Delia planipalpis* (Stein) and *Delia floralis* (Fallén) (Griffiths, 1991a). Larvae feed on roots, forming furrows or tunnels in the main rootstock of a wide range of host plant species, both wild and cultivated. Several other species including *Delia platura* (Meigen) and *Delia florilega* (Zetterstedt) are not primary pests, but contribute to damage after initial attacks by the phytophagous group (Griffiths, 1991a).

1.1.1 Root Maggots and Their Host Plants

The root maggot species *D. radicum*, *D. floralis*, and *D. planipalpis* are oligophagous insects, specialized for completing their development and reproduction on plants of the family Brassicaceae. Brassicaceae comprises about 3,000 species worldwide and occurs primarily in the northern hemisphere. Cultivated crops in this family comprise several cultivars of *Brassica oleracea* L. including cabbage, cauliflower, broccoli, kale, kohlrabi, Brussels sprouts, Chinese cabbage, collards, and several cultivars of *Brassica napus* L. including turnip and swede. More distantly related to these cultivated vegetable crops are the species *Sinapis alba* L. (white mustard) and *Sinapis arvensis* L. (wild mustard). Besides *S. arvensis*, the Brassicaceae also contains a number of weed species (Downey, 1983), including wild radish (*Raphanus raphanistrum* L.), stinkweed (*Thlaspi arvense* L.) and hedge mustard (*Sisymbrium officinale* (L.)). Many brassicaceous weed

species have been shown to support pre-imaginal development of *Delia* spp. In a study by Finch and Ackley (1977), 44 of the 83 species of Brassicaceae tested supported larval development of *D. radicum*. Within this family, the genus *Brassica*, or the mustards, has several economic and commercially grown species. Canola, *B. napus* and *Brassica rapa* L., is grown as an oilseed crop in Canada. Over the past 25 years canola has become established as an important income source and rotational crop for producers throughout Alberta.

In Canada, root maggots are major economic insect pests of canola production (Griffiths, 1991b). Canada produced 4,689,214 hectares of canola in 2003 and Alberta contributed 1,335,463 hectares of that production. In Canada this equates to $1.5 billion dollars annually in farm revenue (Anonymous, Canola Council of Canada, 2005).

1.2 History and Development of Canola

Many *Brassica* species have been cultivated since prehistoric times for their edible roots, stems, leaves, buds, flowers and seeds. History suggests that rapeseed was cultivated as early as the 20th century B.C. in India, and was introduced into China and Japan about 2000 years ago. References to its use or that of a close relative appear in the earliest writings of European and Asian civilizations (Downey, 1983).

Rapeseed plants have the ability to grow at relatively low temperatures with far fewer heat units required than for other oilseed crops (Thomas, 2002). Therefore, rapeseed was one of the very few oil sources that could be successfully grown in the climatic conditions of temperate regions. As a result rapeseed was grown in Europe as early as the 13th century (Anonymous, 1977). Subsequently, rapeseed was used for both

cooking and lighting, as its oil produced a smokeless white flame. Rapeseed had a limited industrial use until the development of steam power, when it was discovered that rapeseed oil would cling to water and steam washed metal surfaces better than any other lubricant. It was this special property that led to the introduction of rapeseed into Canada (Anonymous, Canola Council of Canada, 2005). Rapeseed crushing facilities were first constructed in Canada in 1943 (Anonymous, 1977).

Most plants of the mustard family contain glucosinolates, a group of more than 70 compounds. Glucosinolates are responsible for pungent odor and biting taste, which ranges from the hot flavor in mustard seed and horseradish, to the more subtle flavors of rutabaga and cauliflower. Volatile oils occur in the plants in bound form as a thioglucoside, called glucosinolate, and are hydrolyzed by the action of the enzyme myrosinase, in addition to sulphate ions and glucose, to form an isothiocyanate, nitrile or thiocyanate (Sang et al., 1984).

Glucosinolates in Brassicaceae serve as feeding inhibitors for non-adapted insect species and stimulants for adapted species. These compounds or their metabolites function in four ways, as: 1) anti-fungal agents; 2) feeding deterrents; 3) toxins for some insect herbivores; 4) feeding deterrents or toxins for some wild vertebrate herbivores and some farm animals (Lamb, 1989). Glucosinolate content can be altered by insect feeding. *Delia floralis* larval feeding has been shown to modify concentrations and proportions of glucosinolates in forage and winter oilseed rape (Birch et al. 1990). Ratzka et al. (2002) reported a mechanism, involving the enzyme sulfatase in diamondback moth (*Plutella xylostella* (L.) (Lepidoptera: Plutellidae)), enabling that insect to desulfate glucosinolates, rendering them invisible to the enzyme myrosinase which normally causes the formation

of a variety of toxic hydrolysis products. Natural rapeseed oil also contains erucic acid which is mildly toxic to humans in large doses but is used as a food additive in smaller doses.

The first low erucic acid, low glucosinolate variety of *B. napus* was developed by the University of Manitoba. It was the variety Tower, registered in 1974 (Anonymous, 1977). In 1977, two more "double low" varieties were registered. The first *B. rapa* variety, Candle, was developed by Agriculture Canada, Saskatoon, and the second *B. napus* variety, Regent, was developed by the University of Manitoba. Canada became the first country in the world to produce large quantities of rapeseed with low erucic acid levels in the oil and low glucosinolate contents in the meal (Anonymous, Canola Council of Canada, 2005).

While the rapeseed oil quality changes were being bred into suitable varieties, plant breeders were also working with animal nutritionists to alter the meal quality. Rapeseed meal was an excellent source of protein with a favorable balance of amino acids; however, the use of rapeseed meal in rations was limited by its glucosinolate content because the glucosinolates in rapeseed led to palatability and nutritional problems for livestock and poultry. The glucosinolates break down into other compounds during crushing and feed formulation, resulting in reduced efficiencies when fed to livestock and poultry at high levels in the ration (Downey, 1983).

This new germplasm with improved quality in the seed, oil and meal needed a name to distinguish the commodity from common rapeseed. The term "canola" was adopted. Canola is a genetically altered form of rapeseed, which is one of two species: *B. rapa*, known in Canada as Polish canola, and *B. napus*, known as Argentine canola. The

reduction in glucosinolates in low glucosinolate cultivars is specific to the seed. The term "canola" is now a trademark registered with the Canola Council of Canada and is applied to varieties with less than five percent erucic acid and less than 30 micromoles of glucosinolates per gram of air-dried oil-free meal. Except for high erucic acid varieties destined for specialty industrial markets, the varieties registered in Canada must be of canola quality (Thomas, 2002).

The annual forms of *B. napus* and *B. rapa* are sown in the spring in most of Canada and in northern Europe, but in central and southern Europe and the Pacific northwest of the U.S.A. winter-dormant, biennial forms are sown in late summer (Downey, 1983). The differing phenologies affect the synchronies of the insects found within the crop. Root maggots are significant pests only in the spring-sown areas of North America and Europe (Griffiths, 1986; Alford et al., 2003), although several *Delia* species are widespread pests of the other crucifers throughout Europe and North America (Griffiths, 1991a).

1.3 Biology of Root Maggots

1.3.1 Reproductive Development

The female reproductive system in all Diptera is comprised of meroistic-polytrophic ovarioles (Heming, 2003). The rate of oogenesis varies with species, temperature, relative humidity, and nutritional conditions during larval development. Gibson and Treherne (1916) reported a preoviposition period for *D. radicum* of about six days under laboratory conditions. Caesar (1922) found that females of the cabbage maggot may begin egg-laying four days post emergence and speculated that under

favorable weather conditions that could shorten to two or three days. He also concluded that a female can mature eggs at the rate of 20 or more per day.

Heming (2003) summarized the male dipteran reproductive system as having one sperm tube per testes. Theunissen (1976) reported that *Delia antiqua* (Meigen) (Diptera: Anthomyiidae) required 9-11 days for definitive spermatogonia to develop into spermatozoa.

1.3.2. Eggs and Oviposition

In north-central Alberta, adult *Delia* spp. emerge continuously from their overwintering puparia from mid-May to mid-July, but are most abundant during the latter part of May to mid-June (Dosdall et al., 1996a). Oviposition on canola commences at about the time of stem elongation ("bolting"), usually around mid June (Griffiths, 1986). Female flies begin laying eggs within one week of emerging from their puparia and continue laying eggs for a five- to six-week period (Griffiths, 1991b). Ovipositing females are solitary and usually deposit eggs in small batches near the root collar or on the axils of lower leaves of host plants (McDonald, 1985).

There are conflicting reports in the literature of the number of eggs that a single gravid female is capable of laying. In rutabaga, individual females were reported to produce from 46 to >200 eggs (Nair and McEwen, 1975). Benson (1973) reviewed the population dynamics of *D. radicum* in Canada and England. He reported that females were capable of laying an average of 80 eggs, but in Canada the first-generation females are smaller than those of the first generation in England and laid fewer eggs. Females select plants with larger basal stems for oviposition (Dosdall et al., 1996b), and undergo a

series of spiral flights before oviposition (Finch and Kienegger, 1997). A single fly has been reported to visit 10 plants before locating suitable conditions for oviposition (Caesar, 1922), and has laid as many as 12 eggs in one place. Miles (1953) reported that a female may lay up to 40 eggs per plant and more than one female may choose the same plant for oviposition.

Eggs are small, white and elongate, 0.9 to 1.1 mm long and 0.3 to 0.4 mm across (Hughes and Salter, 1959). Under magnification, each egg can be seen to have many wavy longitudinal furrows and ridges, and on one side there is a deep longitudinal groove (Caesar, 1922). It is along this groove that the larva, when hatching, breaks the shell of the egg and emerges. Eggs are usually laid individually or in small groups. Differences in this longitudinal groove or stripe on the chorion were found between three strains of *D. radicum* (Neveu et al., 1997). The function of this stripe, other than to assist hatching, was proposed as an adaptation to adjust to lower humidity and thus water loss (Neveu et al., 1997). The stripes of eggs of French and Canadian strains were similar in length, 650 μm, but in those of Moroccan strains were only 250 μm long. The viability of the eggs of *D. radicum* is usually 90 to 100% (Harris and Svec, 1966).

Eggs hatch and larvae emerge usually within three to four days of oviposition (Harris and Svec, 1966). Both sunlight and dryness can reduce egg hatch success (Caesar, 1922).

Host location and oviposition are stimulated by the presence of glucosinolates (Coaker, 1970), but the interactions among various glucosinolates and isothiocyanates are also very important (Nair and McEwen, 1976).

Many other plant or soil qualities and characteristics are used by gravid females and contribute to the selection of an oviposition site. Visual detection of their host plants by herbivorous insects has evolved over time, through a coevolutionary relationship (Prokopy and Owens, 1983). Leaf color was demonstrated to be a character used by *D. radicum* before landing on leaves, to discriminate among host plant cultivars of radish, green cabbage and red cabbage. Prokopy et al. (1983) proposed that leaves of cultivated or naturally growing plants that appear whitish to the human eye due to build up of epicuticular wax bloom or pubescence, or that are reddish owing to masking or replacement of chlorophyll by some other pigments, may be less detectable by, or less attractive to, *D. radicum* than are green leaves.

Ellis et al. (1982) found that a complex relationship exists between *D. radicum* and a host plant, involving microorganisms. In their study, adult *D. radicum* laid up to three to four times as many eggs around radish plants grown from untreated (not washed in antibiotics and sodium hypochlorite, NaOCL) seeds as compared to those carrying few or no microorganisms.

The nature of the soil has a major influence on the severity of *D. radicum* infestations through its effects on the plants and the pest (Beirne, 1971). In general, infestations tend to be minimal on dense soils and severe on low-density soils. Traynier (1967a) found that the most favorable soil for oviposition comprised soil particles 1 mm in diameter, which permitted the entry of the extended ovipositor and provided irregularities against which the egg could be laid. Traynier (1967b) also found that oviposition was stimulated primarily by the interplay of many contact chemostimuli by

host plant material. Eggs have also been found on Brussels sprout buttons (Way and Murdie, 1965), so this site must provide both physical and chemical oviposition stimuli.

Studies on the post-alighting behavior of gravid females of *D. radicum* (Kostal and Finch, 1994) and *D. floralis* (Hopkins et al., 1999) determined that complicated behavior patterns influenced host selection and oviposition. Behavioral sequences that include spiral flights around host plants (Kostal and Finch, 1994), proboscis extension, stem standing, walking and running on leaves and stems (Hopkins et al., 1999) all seem to determine whether or not flies will accept the plant for oviposition.

A root maggot oviposition deterrent has been identified in frass of garden pebble moth caterpillars, *Evergestis forficalis* (L.) (Lepidoptera: Pyralidae) (Jones et al., 1988). *Delia radicum* adults were deterred from laying eggs on cauliflower plants sprayed with a water-soluble extract of the frass of caterpillars of the moth, which had fed on a range of cruciferous plants. Spraying plants with a buffered solution of the extract reduced the numbers of cabbage root fly eggs laid by 60-70%. The deterrent effect persisted for five days. An oviposition-deterring pheromone in *Delia* spp. was reported by Zimmerman (1979). His findings detailed the oviposition behavior on flower buds of the perennial herb *Polemonium foliosissimum* Gray (Polemoniaceae). This account has probably arisen from misidentification, as the author never identified the root maggot species and such a mechanism has not previously been described in Anthomyiidae.

There are several methods in the literature that describe sampling or counting eggs, including a washing method (Yaman, 1960), a floatation method (Mukerji and Harcourt, 1970) and *in situ* visual counting (Dosdall et al., 1994).

1.3.3 Larvae of Root Maggots

Root maggot larvae are whitish with two small black hooks for rasping the tissues of the root, thus freeing the juices, which are then absorbed through the mouth near the hooks (Caesar, 1922). At the posterior end of the larvae are a number of small projections or tubercles, of which the two most prominent and central ones are notched or forked at the apex. These forked tubercles are used to distinguish the larvae in keys (Brooks, 1951). There are three larval instars.

First-instar larvae move down the tap-root, penetrate the periderm, and feed on the parenchyma tissue of secondary phloem (McDonald and Sears, 1992). First-instar larvae are 1.5 mm long (Schoene, 1916). Under field conditions, first-instar larval development usually requires about four days (Hughes and Salter, 1959). Larger second- and third-instar larvae aggregate on the root surface, creating progressively wider feeding channels along the root length. Second-instar larvae are about 3.8 mm in length while the third-instar larva can vary, between 2.5 and 8.0 mm in length (Schoene, 1916). Injury is primarily confined to phloem, periderm and xylem parenchyma tissues, but can include the proximal region of the lateral root system in proportion to the level of attack (McDonald, 1985). Under field conditions, second-instar larval development typically requires six days (Hughes and Salter, 1959). Larval identification is accomplished through examination of the number of slits in the posterior and anterior spiracles and determination of the differences in mouthpart structures (Brooks, 1949, 1951). Harris and Svec (1966) reported a pre-pupal stage lasting about three days.

Larval infestation may influence secondary infestations of saprophytic *Delia* species and possibly cause higher overall damage by influencing the glucosinolate

content of roots. Griffiths (1993) inoculated two cultivars of forage rape and one cultivar of oilseed rape with *D. floralis* eggs. Root damage was also simulated mechanically. Larval damage increased the total glucosinolate content of the roots, while mechanical damage did not (it actually reduced glucosinolate content of the roots). Larval damage also modified the glucosinolate composition, with the proportion of indole glucosinolates increasing significantly. Attack by *D. floralis* larvae have also been shown to modify concentrations and proportions of individual glucosinolates in roots (Birch et al., 1990).

1.3.4 The Root Maggot Puparium

The puparium (which encloses the pupa) or resting stage of root maggots is formed by the contraction and sclerotization of the cuticle of the third-instar larva when it is full-grown and has ceased feeding. The puparium is brown, sub-elliptical and rounded (Miles, 1952). The two forked tubercles of the larva can still be seen on the surface and help to distinguish puparia among different species (Caesar, 1922). The puparium varies in length from 3.5 to 6.5 mm (Scheone, 1916).

Pupariation occasionally occurs in the root or tissues of the plant, but most frequently it occurs in the soil surrounding the root. Finch and Skinner (1980) reported that 80% of puparia located deeper than 30 cm failed to have newly eclosed adults successfully reach the soil surface. Klingen et al. (2002) (translating Vasilyevskii, 1929) identified the newly formed puparium as the immature stage most sensitive to infection by pathogenic fungi due to the weakening of the insects defense mechanisms at the time of transformation. The puparial stage is the only stage shown to overwinter. Exposure to temperatures below –10°C reduces survival and affects post-diapause development

(Turnock et al., 1985). The threshold for postdiapause development was reported as 5.6°C (Coaker and Wright, 1963) but recent research determined the base temperatures for development in the soil at 4.0°C for *D. radicum* (Collier and Finch 1985).

1.3.5 Root Maggot Adults

The adult female varies in body color from ash grey to a pale greyish brown with a tint of olive (Caesar, 1922). Adults feed on water and the nectar of flowers (Caesar, 1922), including several non-brassicaceous species like dandelion, white clover, and marsh marigold. Adults were also observed feeding on rotting apples on the ground, on sap exuding from trees, and on aphid honeydew on apple leaves. In cages they feed readily on molasses and water. Gibson and Treherne (1916) indicated that duration of the life cycle of individual adults increased as the season advanced.

Adult dispersal of *D. radicum* within an agricultural field was 8 to 20 m per day (Hawkes, 1972). Hawkes (1972) found that adult flies were not dispersed by wind, but demonstrated a diurnal rhythm in behavior where they left the crop for shelter. Females dispersed more actively than males and were generally more uniformly distributed through the crop (Finch and Skinner, 1973a). Gravid females entered their plots without accompanying males, inferring that they are migratory and mate near the site of emergence. Studies in Canada found a higher capability to disperse, up to 915 m in seven days, and that the presence of a host crop would influence the dispersal rate (Nair and McEwen, 1976). Nair and McEwen (1976) suggested that females have a greater tendency to disperse.

1.3.6 Generations and Diapause

The generation number recorded for most *Delia* species varies. In England (Finch, 1980) and in North America (Mukerji, 1971), *D. radicum* can have two to four generations per year (Griffiths, 1991a). Griffiths (1986) reported that *D. radicum* is univoltine in canola in Alberta. *Delia radicum* adults were first found in pan traps in canola on 11 to 14 May 1985. *Delia floralis* adults were first found in traps from 4 to 7 June 1985, in the same study. Both species showed a pronounced peak in abundance that occurred about 20 June 1985. In studies in the Peace River area of northern Alberta, Broatch (1993) found adults of *D. radicum* and *D. planipalpis* already declining in number by 11 June 1989. *Delia floralis* and *D. platura* had adult population peaks in late June and early July, 1989. A second major peak in mid August was also detected for *D. radicum*, *D. floralis* and *D. planipalpis*, but not *D. platura* which was more abundant on sticky traps in the fall.

Temperature and photoperiod are important cues for root maggot diapause induction (Collier and Finch, 1983b). Read (1969) also included light intensity as a contributing factor. Collier and Finch (1983a) reported post-diapause development once temperatures became sufficiently warm in the spring. The authors believed that the lack of development until warmer temperatures occurred was an adaptive strategy that helped synchronize the spring emergence of the adult population. The temperatures required for post-diapause development and emergence are variable (Collier and Finch, 1983a; Eckenrode and Chapman, 1971; Wyman et al., 1977; Nair and McEwan, 1975; Bracken, 1988), and will be discussed in greater depth in a later chapter.

1.3.7 Host Plant Location

Glucosinolates have been shown to be highly attractive to gravid female *D. radicum* (Nair and McEwan, 1976; Finch, 1978; Finch and Skinner, 1982a, 1982b). *Delia radicum* also responds to plants damaged by conspecific larvae and the odors those plants emit (Baur et al., 1996a, 1996b). Color, intensity and hue can also affect root maggot species attraction (Vernon and Broatch, 1996). *Delia radicum* has been shown to respond to the physiological age of radish, and the preference may be due to chemical composition or physical structure (Ellis et al., 1979).

1.4 Economic Impacts of Root Maggots

Many studies report yield losses from root maggot attacks in commercial cruciferous vegetable crops including cabbage (Getzin, 1978; Vincent and Stewart, 1980) and rutabaga (Read, 1958a). Many of these reports (Dapsis and Ferro, 1982; Doane and Chapman, 1964; Johnson, 1930) link bacterial and fungal infections in crop plants with larval damage. This observation is also relevant to understanding the damage and yield loss observed in canola.

In Canada several economic assessments of root maggot infestations in canola have been conducted (McDonald, 1985; Turnock et al., 1992; Griffiths, 1991b; McDonald and Sears, 1991; Dosdall et al., 1998a; Soroka et al., 2004). Turnock et al. (1992) surveyed commercial fields of canola (*B. napus*) in Manitoba, and found that the level of damage from *D. radicum* increased with increasing precipitation and temperature during June and July and speculated that an extended period of cool, moist conditions could lead to increased damage and possibly to significant yield losses. McDonald and

Sears (1991) concluded that the impact of cabbage maggot on canola was a dynamic process and the correlation of injury with yield was difficult to determine. Larvae can attack conductive and storage tissue between the secondary xylem and the secondary phloem within the periderm. In their study, using *B. rapa,* they concluded that because much of that damage to the canola root system occurred after flowering, the plants were not impaired in their ability to set seed on the primary raceme.

In Alberta, Griffiths (1991b) found exclusion of maggots, achieved through the use of screened cages, increased seed yield by 51.7%, seed weight by 37.6% and protein content of meal by 6.43% in *B. rapa*, and yield increases of 20.2% were observed in *B. napus* protected from damage by root maggots with seed treatments. In this study, the yield impact was less severe when *B. napus* was grown in an area of high fertility. This might imply that yield losses are limited when nutrient constraints or other stress factors are minimized. The association of *Fusarium* foot rot with *B. rapa* was a major consideration in those trials. Dosdall et al. (1998a) found root maggot damage throughout Alberta to be positively and significantly correlated with soil moisture, with areas of high rainfall associated with more severe root damage than areas with low rainfall. Root maggot damage was also correlated with soil type, with regions of most severe infestations found in the black chernozemic soils, while the least severe levels were found in brown and dark brown soil zones. Root maggot damage ratings were associated with seed yield, with the greatest yields obtained where root damage values were low (Dosdall et al., 1998a). Soroka et al. (2004) found that seed yields were not significantly different among cultivars, but that location and year had a major impact on the level of root maggot damage.

The correlation of root maggot feeding to economic damage to canola in the field is often difficult to assess because maggot damage can be associated with several endemic root rot organisms. Griffiths (1986) reported foot rot, involving *Fusarium* spp., occurred in all plants he observed having root maggot damage. Four species of *Fusarium* were identified from cultures grown from the samples. The *Fusarium* species included *F. avenaceum* (Corda ex. Fr.) Sacc., *F. sambucinum* Funckel, *F. tricinctum* (Corda) Sacc., and *F. acuminatum* Ellis and Everh. (Griffiths, 1986). All plants in plots without root maggot damage had green stems and clean white roots at harvest. Griffiths (1986) suggested that feeding by root maggots caused primary damage, facilitating the secondary establishment of root rot organisms.

In general, significant damage occurs in areas where moisture is consistent. Griffiths (1986) mapped the relative abundances of *D. radicum* and *D. floralis* in Alberta. *Delia radicum* was dominant in areas with a mean June-August precipitation approaching or exceeding 250 mm, whereas *D. floralis* was dominant in areas where precipitation was lower. In 1984, Griffiths (1986) found only 1.2% mortality of plants attacked by larvae of *D. radicum*, but Liu and Butts (1982) estimated 13.5% mortality on the same farm in 1981, and a similar level of mortality was suggested by Griffiths in 1983 (Griffiths, 1986). Griffiths postulated that crop mortality in maggot-infested fields occurred when weather conditions favored the spread of *Fusarium* spp. from invasion sites around root maggot wounds.

A western Canadian review (Soroka et al., 2004) found damaged roots in commercial canola fields throughout the survey area. Root maggot infestation levels per field and the degree of feeding injury were similar between the *B. napus* and *B. rapa*

crops surveyed. Root diameter was positively correlated with the degree of root maggot injury, but no clear relationship was observed between infestation levels and yield, degree of injury and yield, or root diameter and yield.

1.5 Control Options for Root Maggots

Control options in vegetable crops include cultural, chemical, and biological strategies, the use of resistant cultivars and direct population reduction through trapping (Finch, 1991). A wide variety of control options have been studied in Canada and are available for canola. A thorough understanding of the dynamics of *Delia* spp. populations is required and should precede attempts at biological, cultural or chemical control if the results of such measures are to be reported or appreciated. In canola the most favorable options include cultural, biological, and chemical control, and resistant canola varieties (Thomas, 2002).

1.5.1 Cultural Control of Root Maggots

Considerable research addressing cultural control of *Delia* spp. has been conducted on vegetable crops and can be found in reviews by Finch et al. (1999), Finch (1991), and Finch and Collier (2000). Cultural control options discussed in these summaries include crop covers, altering sowing, planting and harvesting times, intercropping (Finch, 1991), improved crop hygiene, crop rotation, introduction of new crops, and soil covers (Finch, 1989). Other possible control strategies utilize exclusion nets (Bomford et al., 2000) or oviposition collars (Skinner and Finch, 1986). In canola, seeding date and plant density were investigated and shown to influence *Delia* spp.

infestations (Dosdall et al., 1996b) as well as tillage regimes, row spacing and seeding rates (Dosdall et al., 1998b). Crop fertility could be another management option that influences cabbage root fly damage (Dosdall et al., 2002).

Finch and Skinner (1976) found that by increasing cauliflower plant density, they increased the absolute population of *D. radicum* without affecting cauliflower yields. Beetle predation on their plots also changed with plant density, since most eggs were eaten from egg-caches placed near the high-density plants. Similar work in Canada with canola found that a moderate increase in seeding rates of canola reduced damage and yield loss. Higher plant densities reduced basal stem diameters, which made plants less attractive to egg-laying females (Dosdall et al., 1996b).

Coaker (1969) found that a common method of protecting vegetable crops against cabbage root fly was to vary the times of sowing or planting to ensure that small, highly susceptible plants were not present during periods of peak egg laying activity. Dosdall et al. (1996b) found that root maggot damage declined with late seeding, but under western Canadian conditions and the associated short growing season, the yield advantage gained when plants utilized early-season moisture reserves outweighed the yield loss due to root maggot damage. Plants of both *B. rapa* and *B. napus* seeded in early May had significantly higher root-damage ratings than plants seeded later in the season. Delayed seeding also reduced yield and oil content in *B. napus* but increased meal protein content, while in *B. rapa* yield decreased but oil content increased, protein and meal contents in the later remained the same. Yield increases from early seeding, even with higher root damage, were attributed to the benefits of more favorable growing conditions (Dosdall et al., 1996b). Studies that would elucidate management practices that would

minimize root maggot damage early in the season could lead to corresponding increases in yields.

Tillage prior to seeding reduced the survival of overwintering puparia. Dosdall et al. (1996a) found a decrease in emergence of 55 to 64% for *D. radicum* and 53 to 72% for *D. floralis* infesting canola. Residue management, or reduced tillage, increases the available moisture, which can allow for yield increases even with higher root maggot damage (Dosdall et al., 1998b). General predator abundance follows the gradient of ground cover, which is greater when crop residue is present in reduced tillage systems (Clark et al., 1993). Although Clark et al. (1993) found that most of the common predator species preferred systems with the most ground cover, several species preferred the system with the least ground cover. Other research supports their findings that neither the number of individuals nor number of species were significantly affected by tillage but characteristics of individual species should be carefully considered when evaluating tillage regimes (Tonhasca, 1993). Cárcamo et al. (1995) found that reduced tillage did not significantly change overall carabid activity or species richness but species differed in their responses to tillage treatments. A general review of the influence of conservation tillage on natural enemies can be found in Stinner and House (1990).

Mixed cropping systems of field peas (*Pisum sativum* L.) and canola are being tested in Canada, because they are thought to have agronomic advantages and because the seed of the two crops can be readily separated (Lamb, 1989). This practice is likely to have a substantial effect on the pest complex in canola if experimental results on pest densities in polycultures are borne out (Altieri and Letourneau, 1984; Root, 1973; Tahvanainen and Root, 1972).

Langer (1995) found that the number of *D. radicum* puparia per plant were significantly reduced by the presence of under-sown clover in comparison to a cabbage monoculture. He suggested the "disruptive crop hypothesis" in which the presence of non-host plants disrupts the ability of herbivorous insects to attack their host plants. This hypothesis may also apply to the interaction between parasitoid, host and host plant: with disruption of host plant finding and altered patterns of movement, parasitoid success in host location could be reduced (Langer, 1996). Previously, O'Donnell and Coaker (1975) found similar results with an intra-crop diversity of Brussels sprouts and clover. Soil-dwelling predatory arthropod populations were enhanced by the additional shelter provided by the clover and were responsible for decreased survival of *Pieris rapae* (L.) (Lepidoptera: Pieridae) (30%) and *D. radicum* (60%), although ovipositing root flies may have been deterred from laying eggs around Brussels sprout plants by the clover. O'Donnell and Coaker (1975) found consistent increases in the populations of *Bembidion* spp. (Coleoptera: Carabidae) in these intercrops, which are important predators of root maggot eggs.

In England, oviposition collars have provided good control in cabbage (Skinner and Finch, 1986). In this agroecosystem the three main factors affecting yield loss due to cabbage root fly are the reduction of oviposition, the aggregation of predatory beetles under the collar and the conservation of water around the roots of plants, thus reducing water stress to plants with damaged roots (Skinner and Finch, 1986).

1.5.2 Chemical Control of Root Maggots

Chemical control options are limited in canola. Finch and Collier (2000) reviewed chemical control strategies in vegetable crops.

In canola, Griffiths (1993) utilized several insecticidal seed treatments to evaluate their effectiveness for reducing root maggot infestations. He found an average increase in yield of 10 to 15% over untreated plots, when fertility was not optimal. Griffiths (1993) reported reductions in levels of serious root damage caused by maggot feeding and secondary foot rot of 42% for *B. rapa* and 39% for *B. napus* through the use of Amaze® (oftanol, isofenphos) and Counter® (terbufos) as seed treatments. Significant yield increases were observed in *B. rapa* at both study sites (9.4% at Ellerslie, and 12.1% at Westlock) and in *B. napus* at Westlock (17.8%), in association with seed treatment use. Griffiths believed this confirmed the validity of developing and utilizing seed drill formulations with a delayed release of the chemical formulation to coincide with root maggot hatching. Currently, in Canada, there are no insecticides that list root maggot control in canola on their label. However, Counter® 5G (active ingredient terbufos), provides a reduction in feeding (Brook, 2006).

When using insecticides as a control option it is important to consider the sensitivity of non-target arthropods. Coaker (1966) found that residues of aldrin and dieldrin reduced the number of *Aleochara* spp. (Coleoptera: Staphylinidae) trapped, but increased the numbers of *Bembidion lampros* (Herbst.) probably because their movement was stimulated by the insecticide. Overall he found the reductions of predators, implied by the trapping records, to increase the survival of cabbage root fly eggs and larvae, leading to increased damage to cauliflower, cabbage and Brussels sprouts, which resulted

in yield reductions of up to 70%. Mowat and Martin (1980) found predators provided 43 to 65% reductions in damage to cauliflower roots, but treatment with chlorfenvinphos and chlorpyrifos gave 80 to 92% reductions in damage. Mowat and Martin (1980) did not report the effects the insecticides had on the predator-parasite group, but found the predators and seedbed treatment together gave greater reductions of damage than either control mechanism operating alone.

In Canada, Obadofin and Finlayson (1977) found that *Bembidion lampros* (Herbst.) (Coleoptera: Carabidae) numbers were significantly reduced by foliar applications of methomyl. Dipel® (*Bacillus thuringiensis* Berliner, serovar. kurstaki) and chlorfenvinphos in the soil caused only slight beetle mortality. Cabbage maggot egg numbers laid in Brussels sprouts were reduced by 35, 44 and 66% following applications to the soil of methomyl, *B. thuringiensis* and chlorfenvinphos, respectively. Samsoe-Peterson (1985) found a 100% reduction in egg production of *Aleochara bilineata* Gyllenhal (Coleoptera: Staphylinidae) when subjected to applications of deltamethrin (Decis®) 15 mg a.i./L. Candolfo et al. (1999) evaluated 95 plant protection products including herbicides, fungicides, insecticides, and plant growth regulators to assess the sensitivity of non-target arthropods. *Aleochara bilineata* was involved in 19 of the tested products. When data from herbicides, fungicides, and plant growth regulators were combined, *A. bilineata* had not been affected. However, the insecticides evaluated resulted in 100% mortality of *A. bilineata* during the exposure phase of their study. Hassan (1973) evaluated the effect of insecticides in cabbage and found predation of *D. radicum* was much reduced in insecticide-treated plots compared to controls. Hassan (1973) concluded that carabids and staphylinids significantly reduced cabbage root fly

egg populations in the field, and staphylinid numbers were significantly reduced by insecticide treatments.

1.5.3 Other Control Options

Weather is an important natural factor that influences the success of several stages of development. Hot, dry weather can influence egg hatch. Caesar (1922) found that 89.1% of eggs deposited on or in dry soil, even in the shade, failed to hatch compared with 27.2% in moist soil under the same conditions. Hot dry weather also shortens the life span of adults, both because of temperature and lack of water. It was difficult to keep flies alive in cages for more than three to four days unless the cages were kept in a cool, shaded place and moisture provided (Caesar, 1922).

Host plant resistance has been used successfully to achieve insect pest control in many cropping systems. There are many desirable features of plant resistance from a broader ecological viewpoint. Advantages of host plant resistance include specificity to a pest without a detrimental effect on beneficial insects, ease of adaptation, compatibility with other pest management practices, and harmony with the environment (Kogan, 1988). It is important to recognize and understand the interactions and complementary effects of resistance with other components of an integrated pest management system, such as biological, chemical and cultural controls. All pest management strategies need to be considered and evaluated to ensure compatibility against other potential pest influences in that production system (Dosdall et al., 2003).

There are three fundamental types of host plant resistance to insects: nonpreference, antibiosis and tolerance (Painter, 1951). Antibiosis, a term defined by

Painter (1951), refers to those plant properties that adversely affect the metabolism of an animal feeding on a plant. The adverse effects may range from slower developmental rates to death. Other physiological processes may be affected to various degrees. Antixenosis (Kogan and Ortman, 1978) is a term proposed to replace nonpreference as a form of resistance, because the term nonpreference was more a description of what the insect "decides". Kogan and Ortman (1978) alternatively suggested the term antixenosis to convey the idea that the plant was a poor host. The use of "tolerance" could enable the pest species to build to higher populations that would allow predators and parasites to operate more efficiently (Maxwell, 1991).

There are many examples in the literature where resistance in vegetable crops to *Delia* spp. has been evaluated (Swailes, 1959, 1960; Radcliff and Chapman, 1966; Matthewman and Lyall, 1966). Tolerance has been observed in cauliflower (Coaker, 1969).

Dosdall et al. (1994) evaluated the susceptibilities of four species of Brassicaceae, and various cultivars of canola and mustard, to infestations by root maggots. Based on eggs laid and root injury, they found *B. rapa* significantly most susceptible. Intermediate susceptibilities were found in *B. napus* and *Brassica juncea* (L.), while plants of *S. alba* were the least susceptible. They attributed the mechanism of resistance to antixenosis (or nonpreference), as the root damage was generally correlated with oviposition. Recent work by Dosdall et al. (2000) reported that a genetic basis for resistance to root maggots, which occurs in *S. alba*, could be used to eventually develop new commercial cultivars of canola. The potential for introgressing *S. alba* genes for resistance into *B. napus* varieties for use in an integrated pest management strategy seems optimistic (Kott and Dosdall,

2004). Canola-quality cabbage maggot-resistant genotypes were derived (Kott and Dosdall, 2004), and molecular markers were developed to identify the genes coding for resistance to root maggot attack (Ekuere et al., 2005).

Biological control options include the use of fungi, bacteria, nematodes, parasitoids, predators and sterile insect programs (Finch, 1993). In canola the most likely candidate would be to include enhancement of predator and parasite numbers through integrated pest management practices.

Fungal pathogens have control potential for root maggots, but are usually costly to produce, and individuals within a population often show great variation in susceptibility to infection (Burges, 1981). Finch (1989) reviewed the ecological considerations of using fungi for control options. In the field *Entomophthora muscae* (Cohn) Fresenius (Zygomycetes: Entomophthorales) regularly kills adults of *Delia* spp. A second fungus, *Strongwellsea castrans* Batko and Weiser (Zygomycetes: Entomophthorales) sterilizes the adult flies. Conidia of both fungi are most effective where moisture protects them from desiccation (Finch, 1989).

Thomsen et al. (1999) documented that at least three different members of the *E. muscae* complex naturally infects *D. radicum* in Denmark. Klingen et al. (2000) documented *E. muscae* on *D. floralis* and *D. radicum* in the commercial cabbage ecosystem in Denmark. Other *Delia* spp. including *D. antiqua* in the onion ecosystem (Carruthers and Soper, 1986) and *D. platura* (Tu, 1990) have also been reported as hosts of *E. muscae*. Carruthers (1981) found that adding a second host significantly increased the prevalence of *E. muscae* and its impact on primary pest population. Earlier emergence of *D. platura* allowed *E. muscae* to reach higher levels earlier in the season, and aid in the

control of *D. antiqua* in the onion ecosystem. Temperature, humidity, moisture, wind, sunlight, soil, substrate, pH, pesticides and antimicrobial substances are known to affect host susceptibility and pathogen persistence, transmission, dispersal, development, germination and production (Fuxa, 1987).

Currently, information on which members of the *Entomophthora* spp. complex infect *D. radicum* or *D. platura* in the canola agroecosystem does not exist. I have observed adult *D. platura* and *D. radicum* captured on sticky traps with *Entomophthora* infection symptoms as early as 3 to 10 July. The most obviously infected *Delia* spp. populations, observed as dead carcasses on plants, began 14 July and continued for several weeks (Broatch, personal observation).

Strongwellsea castrans is the only nonlethal member of the Entomophthoraceae. Nair and McEwen (1973) found that infected flies lived a maximum of five to seven days after the appearance of the characteristic abdominal hole through which the conidia are discharged. Their attempts to culture the fungus failed, but under field conditions they found a high infection rate associated with high relative humidity and possibly a comparatively low temperature. This observation was also reported by Lamb and Foster (1986) in Scotland. They found the greatest sustained infection levels were recorded in the coolest, wettest season. They also attributed some of the higher levels recorded there to the observation that both *D. radicum* and *D. floralis* were infected. In Scotland, *D. radicum* had a July generation, while *D. floralis* had an August generation (Lamb and Foster, 1986). Up to 27 and 34% infection rates were recorded in July and August, respectively. They did not associate the disease with the growing of brassicaceous crops, as high levels of the disease were found in rotations with cereals or grass.

Finch et al. (1999) reported that a soil-inhabiting fungus, *Metarhizum anisopliae* (Metsch.) Sorokin (Deuteromycotina: Hyphomycetes) attacks the fly larvae rather than the adults and should be evaluated for cabbage maggot control. Attempts to control root maggots with other entomopathogenic fungi were evaluated by Vanninen et al. (1992). They reviewed *M. anisopliae*, *Paecilomyces fumosoroseus* (Wize) Brown and Smith (Deuteromycota: Hyphomycetes) and *Beauveria bassiana* (Bals) Vuill. (Ascomycota: Clavicipitales), all members of the Hyphomycetes. In general they found that control in laboratory and greenhouse conditions was limited, with 40 to 50% mortality of both *D. floralis* and *D. radicum*. The authors concluded that the concentrations needed for efficient control may be too high for economic and environmental viability (Vanninen et al., 1992).

Recent work in Europe (Klingen et al., 2002) evaluated several other hyphomycetous fungi, *Tolypocladium cylindrosporum* Gams, *M. anisopliae* and *B. bassiana*, for effective control of *D. floralis* larvae. They obtained 36% mortality of larvae with *T. cylindrosporum*. Larsson et al. (1995) described *Cystosporogenes deliaradicae* n. sp (Microspora, Glugeidae) as a microsporidian parasite of *D. radicum* and *D. floralis* in Denmark.

The use of the delta endotoxin from the bacterium, *B. thuringiensis*, to control *D. radicum* and *D. floralis*, has been evaluated in cabbage (Havukkala, 1982). The use of *B. thuringiensis* reduced root damage in two years out of four. Parasitism by *Aleochara* spp. in *B. thuringiensis*-treated plants was one-third that of untreated plants. Havukkala (1982) proposed that conditions such as soil pH, soil type, nutrient levels and harmful effects on natural enemies need to be studied further.

The results of experiments with nematodes and their effectiveness against *Delia* spp. have been inconsistent (Finch, 1991). Most of these experiments were carried out under conditions designed to optimize nematode success but were sub-optimal for the pest species. Morris (1985) evaluated the susceptibility of a wide range of agricultural insect pests to the entomophagous nematodes *Steinernema feltiae* Filipjev and *Heterorhabditis bacteriophora* Poinar, and found that *D. radicum* and *D. antiqua* were moderately susceptible. Dosages of 125 nematodes per insect larva killed 80% of *D. radicum*, while 83 nematodes per larva killed 100% of *D. antiqua*. He also noted that these *Delia* species would be good candidates for control by nematodes as oviposition and egg hatching occurred near the soil surface where larvae are exposed to nematodes applied as a spray. The parasitic nematode, *Steinernema carpocapsae* (Weiser), attacks a variety of soil-inhabiting insects, including larval cabbage maggots. The nematode populations that occur naturally in the soil are not usually high enough to provide control, but nematodes can be released as biological insecticides. A high concentration of nematodes (as many as 7.5 billion per ha) and optimum conditions for infection are required to control cabbage maggots (Finch, 1991). Finch (1991) recommended that testing be conducted under conditions as similar as possible to those of the insect's natural environment, because even plant breakdown products could influence nematode infestation success.

Sterile insect programs, utilizing a chemosterilant bait (tepa, [tris-(1-aziridinyl) phosphine oxide]) and sterile male release have been evaluated (Finch and Skinner, 1973b). Protracted immigration, an innate tendency for females to disperse, reduction in the competitiveness of sterile males, and the failure of males to re-disperse once sterilized

seemed to be the main factors limiting the effectiveness of this approach in the field. Finch and Skinner (1973b) obtained as high as 94% sterility in populations in large field cages, but the sterility of eggs rarely exceeded 30% in the field. The release of sterile insects was no more effective than using baits.

The most important and widespread parasitoids of *D. radicum* in North America and Europe are *Aleochara bilineata* Gyllenhal (Coleoptera: Staphylinidae) and *Trybliographa rapae* (Westwood) (Hymenoptera: Cynipidae) (Griffiths, 1991a). Klimaszewski (1984) also reported *Aleochara verna* Say and *Aleochara curtula* (Goeze) as reared from *D. radicum*. Recent samples collected in Alberta and sent to Klimazewski identified *A. bilineata* as the species emerging from puparia collected in canola at Lacombe and the Vegreville/Westlock areas (J. Klimaszewski, personal communication). Klimazewski (1984) reported the first-instar larvae of *A. bilineata* attacking *D. radicum, D. platura, D. floralis, D. planipalpis* and other Anthomyiidae and also Calliphoridae. *Aleochara bilineata* will be discussed in greater depth in a later chapter.

Trybliographa rapae has been identified as a parasitoid of a wide range of hosts including *D. radicum, D. floralis,* and *D. platura* (Wishart and Monteith, 1954), and it is known from both western and eastern North America (Wishart and Monteith, 1954; Hemachandra, 2004). The female of *T. rapae* is a koinobiont endoparasitoid that can parasitize and develop in all three larval instars of *D. radicum* (Jones and Hassell, 1988; Tamer, 1994), and there is no difference in acceptance between the three stages unless larval densities are high (Neveu et al., 2000). However, they also found that if the three stages were offered simultaneously, *T. rapae* preferentially parasitized the third instar. The development time, as well as body size of the parasitoid, depends on the host's stage

of development (Neveu et al., 2000). Reported developmental requirements are 1.40°C and 1.45°C as the developmental threshold for second and third instars respectively (Kacem et al., 1999). Kacem et al. (1999) also reported that 1000 and 909 degree-days were required for each of those developmental threshold temperatures respectively, with males generally developing faster than females.

Adult *T. rapae* are not active fliers (Wishart and Monteith, 1954). The adult female is attracted to host volatiles from host roots infested with *D. radicum* larvae (Neveu et al., 2002). Females were also attracted to undamaged parts of infested roots and even undamaged leaves. Neveu et al. (2002) attributed this attraction to elicited volatiles caused by the host larvae and termed them herbivore-induced volatiles. These volatiles would be important long distance host location cues.

Langer (1996) found that parasitism by *T. rapae* was not consistently affected by the level of ground cover. Parasitism by *T. rapae* was also unaffected by a mulch of grass clippings (Hellquist, 1996). Block et al. (1987) reported *D. radicum* puparia were parasitized by *T. rapae* as deep in the soil as 10 cm, but overall parasitism at that depth was only 4.5% versus 40.1% at 0-2.5 cm. *Trybliographa rapae* larvae overwinter as fourth instars within host puparia.

Females locate their host larvae through three behaviors: antennal searching, ovipositor probing and vibrotaxis (Vet and van Alphen, 1985). A description of the egg, first, second, third and fourth larval instars and the pupa are given by Kacem et al. (1996). The third instars are ectoparasitic, in contrast to the first two instars which are endoparasitic. Third instars exit the host pupa by chewing their way out, consuming the host pupa from the outside, but within the host puparium. The parasitoid then develops

into a grub-like larva and overwinters (Block et al., 1987). After developing through the fourth instar and pupal stages, the adult wasp cuts an exit hole and emerges (Wishart and Monteith, 1954).

Other hymenopteran parasitoids attack larval cabbage maggots and emerge from the puparia. The ichneumonids, *Phygadeuon fumator* (Gravenhorst) and *Atractodes tenetricosus* (Gravenhorst), and the braconid *Aphaereta auripes* (Prov.), are found occasionally, but never contribute substantially to cabbage maggot mortality (Wishart, 1957).

Caesar (1922) listed *Aleochara anthomyie* Sprague (Coleoptera: Staphylinidae) as a root maggot predator and parasitoid. Besides *A. anthomyie* he found three species of small "4-winged flies", *Conthonaspis (Hexaplesta) gillettei* Wash, *Serphus* sp. and *Belytra* sp. Caesar (1922) proposed that the latter two could be either parasites or hyperparasites. In 1919, from 1120 overwintering puparia, 443 of the tiny "4-winged flies" were reared and 16 rove beetles emerged. Possibly more than one of the small parasitoids could emerge from a single puparium. Caesar's description of the parasites as "4-winged flies" is confusing, and were likely Hymenoptera; however, with such high levels of parasitism his report is important.

Various Staphylinidae and Carabidae have been reported to be predators of insect pests, as reviewed by Norris and Kogan (2000). Their report associated higher ground beetle numbers with weedy situations, and identified plant cover as a support for increased activity of the predators. Predation of eggs and larvae by staphylinid and carabid beetles is known to be important in population regulation of *D. radicum* (Coaker, 1965). Research in Ontario by Wishart et al. (1956) with *D. radicum* found predation on

eggs by carabids to be responsible for the highest level of predation, with staphylinids also of some importance. Wishart et al. (1956) found the carabid *Bembidion quadrimaculatum oppositum* Say to be the most abundant predator with the highest egg-eating capacity. Another carabid, *Bembidion nitidum* Kirby, was also highly successful.

In Ontario, Caesar (1922) found that the primary predaceous enemies of *D. radicum* were a large red mite, six species of small rove beetles and four species of ground beetles. The mite was observed feeding on eggs and was fairly abundant throughout the growing season.

Finch (1996) conducted laboratory studies to determine the number of eggs of *D. radicum* consumed by 60 species of ground beetles collected from a range of habitats. A linear relationship was observed between the number of eggs consumed and beetle length, for 35 species that ranged in size from 2.7 mm to 10.0 mm long. There was great variability in the number of eggs eaten once the beetles were larger than 10 mm, and 10 mm seemed to be the upper size limit of carabid predators of cabbage maggot eggs.

The abundance and activity of ground beetles is influenced by crop type. Even surrounding fields, hedges and tree rows influence carabid fauna (Hance et al., 1990). Hance et al. (1990) found that adjacent habitats play a role for species sensitive to agricultural practices. Studies comparing bio-dynamic, organic and conventional farming found that, compared to conventional plots, the bio-dynamic plots contained 1.93-fold more epigaeic arthropods, while the organic plots had 1.88–fold more arthropods. Activity of carabids, staphylinids and spiders was higher in the bio-dynamic and organic plots (Pfiffner and Niggli, 1996). The treatments (bio-dynamic, organic, conventional)

differed mainly in plant protection management and fertilization, organic versus mineral fertilization, and level of management intensity.

Feeding by Carabidae on eggs can be important limiting factors for root maggot populations. When exclusion techniques reduced carabid populations by an estimated 72%, *D. radicum* egg survival increased by 50% (Wright et al., 1960). Similarly, in the U.S.A. a decrease of 44% of *B. quadrimaculatum* was associated with a 55% increase in egg numbers (Pitre, 1965), and in Ireland 59% fewer carabids were associated with a 52% increase in egg numbers (Ryan and Ryan, 1980). When carabid numbers were lowered by insecticides, root maggot egg numbers also increased (Coaker, 1966).

Ellsbury et al. (1998) found that reduced chemical inputs encouraged greater abundance and diversity of beneficial carabids than found in high-input plots without the loss of yield seen in the low-input plots. Their plots evaluated treatments maintained under high, managed and low levels of chemical fertilizers and pesticide inputs. More information on Carabidae and their influence on root maggot populations will be presented in a later chapter.

In western Canada there is a paucity of information describing the carabid fauna in canola. Several research reports list carabid species (e.g., Frank, 1971; Doane, 1981), but comparisons of populations over time have been few. There have been introductions from Europe, such as *Pterostichus melanarius* (Illiger), *Clivina fossor* (L.) and *Carabus granulatus* L., and those introductions can influence the indigenous community of ground beetles (Lindroth, 1969).

Read (1962) observed *Scatophaga stercoraria* (L.) (Diptera: Anthomyiidae) destroying adult *D. radicum* in a caged study in Prince Edward Island. Read (1958b) also

reported it from collections in rutabaga fields throughout P.E.I. and northeastern Nova Scotia in 1957, and reported that it was often more abundant than *D. radicum.*

1.6 Root Maggots and Weeds, and the Focus of This Research

The presence of weedy backgrounds can provide cover for predators searching for herbivorous hosts and completely removing those weeds at early stages of canola development could predispose crop plants to greater damage by herbivores later on because natural enemies may have migrated away from those sites. Kromp (1989) found that numbers of carabid beetles (Coleoptera: Carabidae) were higher in biologically managed fields due to their greater weediness and heterogeneity, and the absence of pesticides. For carabids, the differences between treatments were most pronounced in spring. Vegetational diversity influenced carabid species responses due perhaps to such factors as prey availability and microclimatic preferences (Pavuk et al., 1997).

Weeds provide much of the plant diversity within and outside of crop fields, improving the availability of hosts for beneficial arthropod predators and parasites, and shelter for many important beneficial species (Altieri and Whitcomb, 1979). In a major review, Norris and Kogan (2000) summarized several studies on weeds in managed ecosystems but cautioned that most interactions are species-specific and may change when the natural enemy species involved change. Banks (2003) reviewed several strategies regarding the influence of plant diversity on herbivores and natural enemies and demonstrated that manipulating plant diversity within agroecosystems can be an effective component of insect pest control strategies. These summaries highlight our need for additional studies in the canola agroecosystem. In a recent study in canola, Dosdall et al. (2003) found that damage to canola taproots and oviposition by root maggot females

declined by approximately 6 and 23%, respectively, with a delay in weed removal from the two- to six-leaf stages of canola development. The most plausible explanation for this effect related to the disruption by weeds of the behavioral sequence of events that precedes oviposition in mated, gravid female flies.

Late-emerging weeds usually have little negative impact on crop yield, and their contribution to the weed seed bank in soils is often insignificant (O'Donovan, 1994); nevertheless, many growers routinely apply herbicide to control these weeds. My research aims to investigate the effect of reducing herbicide application rates as a key to improved integrated crop management: with a small weedy background derived from lowered herbicide application rates, infestations of insect pests should decline, resulting in improved environmental and economical sustainability. Of course a major key to the success of this strategy is determining the level of weedy background that enhances the management of insect pests, but does not cause excessive interspecific competition between weeds and crop plants.

My research focuses on managing root maggot infestations from a new holistic direction, and should result in substantial benefits to producers. My hypothesis is that reduced herbicide application rates, relative to the full recommended application rate, in canola at the two- or four-leaf stages of development will kill sufficient numbers of weeds to reduce crop losses from interspecific competition, but yet provide enough cover for natural enemies to reduce root maggot infestation levels or influence root maggot damage. If my hypothesis withstands the rigors of objective, replicated field experimentation, it should result in recommendations to growers to apply less herbicide,

thereby enhancing economic returns, and contributing toward holistic crop management in canola.

The objectives of my study are:

1. to determine the effects of reduced herbicide application rates on populations of monocotyledonous weeds and associated canola crop damage from root maggot infestations and the effects on weed and root maggot dynamics in canola;
2. to determine the degree-day requirements, Julian Date associations and population dynamics of the root maggots *D. radicum* and *D. platura* and their principal parasitoid, *A. bilineata* in canola agroecosystems; and
3. to determine the effects of reduced herbicide application rates and associated weed populations on the natural enemies of the root maggots *D. radicum* and *D. platura,* specifically carabid beetles and *A. bilineata*.

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Chapter 2: Using Degree-day and Logistic Models to Predict Emergence and Flight of *Delia radicum* (L.) and *Delia platura* (Meigen) (Diptera: Anthomyiidae) in Canola[1]

[1] *Note*: A version of this chapter has been published:

Broatch, J.S., L.M. Dosdall, G.W. Clayton, K.N. Harker and R.-C. Yang. 2006. Using degree-day and logistic models to predict emergence patterns and seasonal flights of the cabbage maggot and seed corn maggot (Diptera: Anthomyiidae) in canola. *Environmental Entomology* 35: 1166-1177.

2.1 Abstract

Flight activity periods and emergence phenologies of the cabbage maggot, *Delia radicum* (L.), and the seedcorn maggot, *Delia platura* (Meigen) (Diptera: Anthomyiidae), were investigated from 2002 to 2004 in plots of canola (*Brassica rapa* L. and *Brassica napus* L.) in central Alberta, Canada in relation to degree-days (DD) and Julian date (JD). *Delia radicum* was univoltine in canola. Peak emergence occurred after approximately 345.8 ± 79.4 DD (± S.E.), and 50% flight activity required ca. 324.5 ± 46.8 DD (soil base 4°C). *Delia platura* was bivoltine in canola. Peak emergence of the first generation required approximately 339.5 DD, and the second generation required ca. 594.5 ± 38.9 DD (soil base 3.9°C). Peak flight activity occurred after approximately 255.0 ± 74.2 and 639.9 ± 69.4 DD for the first and second generations, respectively. A logistic model, constructed to describe the relationship of DD and JD with emergence patterns of adult flies, predicted that 10, 50, and 95% emergence of *D. radicum* required 213.7 ± 39.9, 324.5 ± 46.8, and 467.2 ± 46.3 DD, respectively. Logistic analysis

predicted that 50% emergence of the first generation of *D. platura* required an average of 255.0 ± 74.2 DD, and the second generation required 526.8 ± 66.6, 639.9 ± 69.4, and 952.8 ± 77.0 DD for 10, 50 and 95% emergence respectively. Determination of the temporal patterns of abundance of *D. radicum* and *D. platura* has considerable potential for pest management because it can enable growers to time canola seeding to avoid synchronization between host plant growth stages vulnerable to oviposition during peak flight periods of these pests.

2.2 Introduction

The cabbage root maggot, *Delia radicum* (L.) (Diptera: Anthomyiidae), is oligophagous on Brassicaceae, Holarctic in its distribution, and a pest of considerable economic importance, especially in the production of cole crops in the Palaearctic region (Griffiths, 1991a). In vast regions of the Canadian prairies, the cabbage maggot is a significant pest of canola (*Brassica rapa* L. and *Brassica napus* L.) (Griffiths, 1991b) capable of causing severe economic losses when larvae feed on the conductive and storage tissues of the taproot, disrupting the transport of water and nutrients between the root and upper regions of the plant (McDonald and Sears, 1992). Root maggot infestations can be associated with leaf and stem wilting, poor seed set, and in severe infestations, killed plants with roots completely severed (Griffiths, 1986a; McDonald and Sears, 1992). The seed-corn maggot, *Delia platura* (Meigen), is polyphagous and the most widespread and abundant species of *Delia* worldwide, occurring in all continents except Antarctica (Griffiths, 1991a). In canola it is believed that larvae of *D. platura* are secondary feeders on damaged taproot tissues following primary attack by larvae of *D. radicum* or *Delia*

floralis (Fallén) (Griffiths, 1986a, b). In recent surveys, root maggot damage occurred in 96% of commercial canola fields in Manitoba and Saskatchewan and 99.8% of fields in Alberta (Soroka et al., 2004). Soroka et al. (2004) reported that estimated yield losses could be as high as $100 million (Can.) annually. Both *D. radicum* and *D. platura* are hosts for the staphylinid predator-parasitoid *Aleochara bilineata* Gyllenhal (Coleoptera: Staphylinidae) (Klimaszewski, 1984); therefore, phenologies of both *Delia* species are of interest in determining agronomic practices that benefit populations of natural enemies and thereby reduce the impact of these pests.

Understanding temporal patterns of abundance of *Delia* spp. in canola agroecosystems is an important prerequisite for formulating appropriate management strategies. The phenology of *Delia* spp. can vary among agroecological regions depending on the species composition and abundance of the *Delia* species present, and regional risk forecasts need to take into account the emergence characteristics of local populations. Under field conditions, generation time can be influenced by microclimatic factors, population genetics, and host quality (Pitcairn et al., 1992). Developmental predictions using degree-day (DD) models can be used to improve the timing of chemical, biological, and cultural control procedures (Dent, 2000). For example, canola growers can manipulate crop phenology by altering seeding date (Thomas, 1990). Canola is more susceptible to infestation by *Delia* spp. at some developmental stages than at others (Griffiths, 1986a; Dosdall et al., 1994), so knowledge of DD requirements for emergence can be very useful when altering seeding date as a cultural control strategy. Information on the phenology and DD requirements of *Delia* spp. and other pest species allows researchers and producers to explore and utilize relationships that might exist

where agronomic strategies such as seeding date, varietal choice, and pesticide applications could influence those pest populations.

DD models have been used to assist in the development of control strategies for *D. radicum* in England (Collier and Finch, 1985), Wisconsin (Eckenrode and Chapman, 1971, Eckenrode and Chapman, 1972, Wyman et al., 1977), and New York (Jyoti et al., 2003), and for *D. platura* in Iowa (Funderburk et al., 1984) and Ohio (Hammond, 1995), but little phenological information has been developed for these species in Canada, especially in canola. In this study, we investigated emergence of *D. radicum* and *D. platura* in relation to DD development, as a key to improved monitoring and forecasting of invasions of canola crops.

2.3 Materials and Methods

2.3.1 Study Site

Experiments were conducted at the Agriculture and Agri-Food Canada Research Station, Lacombe, AB (113°44′W; 52°28′N). Soils at the site developed on glacial lacustrine deposited material (Bowser and Peters, 1951). Plots seeded to *B. napus* and *B. rapa* were on black Chernozemic clay loam soil (43% sand, 21% silt, and 36% clay) with a pH of 5.9 and 8.2% organic matter content.

2.3.2 Monitoring of Adult Flight

Delia spp. populations were monitored with yellow sticky cards (Phero Tech Inc., Delta, BC) from spring through fall of 2002 to 2004. The cards were bright yellow, 7 by 13 cm in size, and were covered on both sides with adhesive. The cards were held 30 cm

above ground level by attaching them with staples to wooden stakes; for consistency each card was placed 1.5 m from the front of the plot, and 1.5 m from the left edge of the plot. Monitoring was performed weekly from 18 June to 30 August 2002, from 22 May to 8 August 2003 and from 21 May to 11 August 2004.

2.3.3 Monitoring of Adult Emergence

Delia spp. emergence was monitored in 2003 with pyramidal traps that were set onto soil seeded in the previous year to canola, and known to harbor root maggot puparia. The traps followed the design of Dosdall et al. (1996), and were set out in early April of each year on plots harvested in the preceding autumn. Each trap measured 1 m^2 at the base, and was covered in fine mesh screening to prevent escape of insects emerging from within the traps. The traps were dug into the soil and sealed at the bottom. Newly eclosed *Delia* spp. adults were captured weekly from one emergence trap per plot with a sticky card suspended within the trap from its upper frame, and from the other trap per plot with a battery-powered aspirator (Hausherr's Machine Works, Toms River, NJ) inserted through an opening in the side of the trap. These openings were sealed except during sample collections.

2.3.4 Species Identifications and Voucher Specimens

Identifications of *D. radicum* and *D. platura* were performed using Brooks (1951) and Griffiths (1991a), with representative species identifications verified by G.C.D. Griffiths (personal communication). Voucher specimens from the study have been

deposited in the Strickland Museum of Entomology, University of Alberta, Edmonton, AB.

2.3.5 Degree-day Calculations

DD calculations were computed using the equation (2.1):

$$DD = \frac{(Tmax + Tmin)}{2} - (Tbase) \times 1 \text{ day} \qquad (2.1)$$

where T_{max} is the daily maximum temperature (°C), T_{min} is the daily minimum temperature, and T_{base} is the base temperature for insect development (Arnold, 1960). Base temperatures for soil were 4°C for *D. radicum* (Collier and Finch, 1985) and 3.9°C for *D. platura* (Funderburk et al., 1984). The DD accumulation was derived from temperatures recorded on a Campbell Scientific CR10 data-logger (Campbell Scientific Canada, Edmonton, AB). Soil temperatures were obtained at a depth of 5 cm and were measured with a Type E thermocouple. The air sensor was held in an R.M. Young 12 gill plate radiation shield. Temperature data were obtained and recorded every 5 min.

2.3.6 Logistic Model

Based on the number of DD and Julian day (JD) calculations, a logistic model was constructed to describe the relationship of DD or JD with the emergence patterns of adult flies for the spring generation of each year and the combination of both years. This model was then used to predict the total DD and JD from emergence of 10, 25, 50, 75, and 95% of the flies for the spring generation. We employed the following equation (2.2) for the logistic model of Jyoti et al. (2003):

$$Y = a + \frac{c}{1 + \exp\{-b(x - m)\}} \qquad (2.2)$$

where Y is the percent emergence, x is either the summation of JD or DD, a is the lower asymptote, c is the upper asymptote, m is the JD or DD requirements for maximum emergence (or inflection point) and b is the slope. This model has been shown to fit temperature development of poikilothermic animals (Davidson, 1944) and has been used to describe the emergence of overwintering populations of *D. radicum* (Jyoti et al., 2003).

2.3.7 Data Analyses

Means and standard errors used in graphs or tables describing the adult captures from all traps per week for each year were calculated using PROC MEANS (SAS Institute Inc., 2004). Estimates of the four parameters (*a, b, c* and *m*) as given in the logistic model were obtained through PROC MODEL (SAS Institute Inc., 2004). Logistic calculations of the percent emergence of populations were calculated with Microsoft Excel® computer software.

2.4 Results

2.4.1 Environmental Conditions and Plant Development

Precipitation during the 2002 and 2003 growing seasons was much below average, especially during June and July (Table 2.1). However, precipitation patterns during 2004 were much closer to long-term mean values. Root maggot infestation levels are correlated with soil moisture content (Griffiths, 1986b), and drought in 2002 and 2003 was not conducive to development of significant root maggot infestations. Mean temperatures during this period were slightly above the long-term averages during June

and July of 2002 and 2003 (Table 2.1). Residual soil moisture levels from snow melt were sufficient to ensure uniform germination and emergence of canola seedlings.

2.4.2 Adult Flight Patterns

Delia radicum and *D. platura* were the dominant root maggot species collected on sticky traps comprising approximately 30 and 62% of all Anthomyiidae specimens, respectively. Other anthomyiids caught on the traps in each year included *Delia florilega* (Zetterstedt), *Botanophilus fugax* Meigen, and *Adia cinerella* (Fallén). At times when the latter three species were most abundant, they could comprise as much as ca. 1, 2, and 5% of all anthomyiids, respectively. Very low numbers of several other grass root-feeding Anthomyiidae also were captured on traps.

In 2002 more *D. radicum* than *D. platura* were captured overall, but in the following two years, *D. platura* dominated total trap captures. Considering all three field seasons, *D. platura* was more abundant than *D. radicum*, but the two species were separated temporally. Peak flight of *D. radicum* occurred in June whereas *D. platura* occurred in relatively low densities on trap samples until July when densities increased to one or two peaks. In 2004 trap captures of *D. platura* demonstrated an additional peak in June.

Total DD soil base 4.0°C accumulations over the three years, until harvest on 15 August, were somewhat variable, and were reflected in the calendar and JD insect phenologies. The total DD at soil base 4.0°C for 2002, 2003, and 2004 were 955.4, 1070.5, and 1130.2, respectively; total DD accumulations at soil base 3.9°C were 965.1, 1081.2, and 1142.4, respectively.

In 2002 a total of 1,636 *D. platura* were captured. Trap numbers were near zero early in the season until early July when *D. platura* populations increased rapidly to a peak of approximately 3.5 adults per trap per d (Figure 2.1). Over the next 21 d, trap captures declined nearly three-fold, but then increased to a second, smaller flight peak in mid August. By late August, numbers declined nearly to zero. Peak emergence of *D. platura* from 9 to 12 July (JD 190-193) corresponded to 496 to 592 DD (mean 544) (soil base 3.9°C). The second population peak from 6 to 9 August (JD 219-221) corresponded to 876 to 903 DD (mean 889.5). Males were captured more frequently than females (82% males versus 18% females throughout the season), but peaks in trap captures were aligned temporally between the sexes. Assuming that the two population peaks indicated distinct generations, 345.5 DD accumulated between the mean of the two generations for soil-based temperatures.

In 2003, a total of 7,239 *D. platura* were captured. Numbers were very low from late May to early July when populations increased rapidly to a maximum of approximately 4.5 per trap per d (Figure 2.1). High densities were maintained on the traps for approximately 14 d, but thereafter adult flight declined rapidly nearly to zero by early August. Proportions of males and females collected in the traps were approximately equal until early July, but for about the next 20 d, male captures were approximately twice those of females. By the end of the season, proportions of males and females were approximately equal. Throughout the season, 65% of specimens were males and 35% were females. Peak emergence of *D. platura* from 2 to 16 July (JD 184 to 198) corresponded to 480 to 657 DD (mean 568.5) (soil base 3.9°C). Both female and male captures peaked during this period.

In 2004, a total of 1,124 *D. platura* specimens were collected. Adult numbers were low throughout May, but increased to a peak in mid June with a mean of approximately 3.0 per trap per d (Figure 2.1). Populations then declined to low levels by the end of June, but then increased approximately five-fold in mid July and numbers remained high until early August. By mid August, numbers declined nearly to zero. Peak emergence of *D. platura* from 10 to 16 June (JD 163 to 168) corresponded to 314 to 365 DD (mean 339.5) (soil base 3.9°C). The second population peak during 7 to 14 July (JD 189 to 196) corresponded to 631 to 711 DD (mean 671). Peaks of both females and males occurred during these two periods. Assuming that the two population peaks indicated distinct generations, DD accumulations between the generations were 331.5 for soil base values. Populations of the second generation remained high until early August. There may have been a third overlapping peak from 21 July to 4 August (JD 203 to 217) corresponding to 906 to 1010 DD (mean 958). This allowed a DD accumulation between means of capture peaks of 287.

In 2002, a total of 2,202 *D. radicum* were captured. Throughout the season, males were captured more frequently than females (80% males versus 20% females), but peaks in trap captures were aligned temporally between the sexes. Peak emergence of *D. radicum* from 25 to 28 June (JD 176-179) corresponded to 316 to 358 DD (mean 337) (soil base 4.0°C). During this period, adults numbered approximately 13 per trap per d (Figure 2.2). Populations declined rapidly in early July and remained low for the remainder of the season, with only a marginal increase in August. Most captures in August were males.

In 2003, a total of 2,053 *D. radicum* adults were collected, and mean numbers per trap were much lower than in 2002. Early in the season, trap captures increased rapidly to a peak of approximately 1 per trap per d in early June (Figure 2.2). Thereafter adult flight declined rapidly to nearly zero by early July, but with few specimens collected in late July. Peak emergence of *D. radicum* from 5 to 12 June (JD 156 to 163) (mean 159.5) corresponded to 181 to 245 DD (mean 213) (soil base 4.0°C). Male numbers peaked during this period, but females peaked in the following week. However, for the entire season the proportions of males and females were approximately equal (52% male, 48% female).

In 2004, a total of 238 specimens of *D. radicum* were collected. Adult numbers were low throughout May, but increased to a peak in late June when a mean of approximately 2 per trap per d were collected (Figure 2.2). Populations then declined to low levels by the end of June, but then increased slightly in mid August. Peak emergence of *D. radicum* from 23 to 30 June (JD175-182) (mean 178.5) corresponded to 440 to 535 DD (mean 487.5) (soil base 4.0°C). Both female and male captures peaked during this period. A small population increase was evident in mid August and comprised predominantly males (79% male, 21% female). Overall captures of males and females throughout the season were approximately equal (48% male and 52% female) (Figure 2.2).

2.4.3 Adult Emergence Trap Patterns

Total emergence trap collections of *D. platura* were lower than for *D. radicum* (71 versus 183 specimens) in 2003. Numbers of males and females of *D. platura* were

low in late May, but increased to a peak from 30 May to 6 June (JD 150-157), corresponding to 131 to 194 DD (mean 162.5) (soil base 3.9°C) (Figure 2.3). A second peak from 20 to 27 June (JD 171-178) corresponded to 345 to 412 DD (mean 378.5). A small peak from 18 to 25 July consisted primarily of females. Overall emergence trap captures comprised 37% males and 63% females, with peaks in trap captures generally aligned temporally between sexes.

Emergence of both males and females of *D. radicum* peaked from 13 to 20 June (JD 164-171), corresponding to 255 to 340 DD (mean 297.5) (soil base 4.0°C) (Figure 2.4). Males were captured in slightly higher numbers from early June until that peak, whereas females were somewhat more abundant in the late June to early July collections. Overall emergence trap captures were 53.5% males and 46.5% females.

2.4.4 Prediction of DD and JD requirements

Nonlinear Ordinary Least Squares parameter estimates, JD, and DD for *D. platura* from logistic analyses (soil base 3.9°C) are summarized in Table 2.2 for 2002-2004. Using these values, the DD requirements of *D. platura* for 25 to 75% emergence ranged from 475.6 to 605.4, and JD estimates ranged from 188.7 to 197.8 (Table 2.3).

Parameter estimates from logistic analysis for the overwintered population of *D. platura* in 2003 were not attainable from the logistic analysis due to limited data. With only four trapping periods, the logistic curve parameters could not be estimated. However, estimates from two trapping periods indicated that 180.8 and 244.6 DD, or JD 156.0 and 163.0, were associated with 50 and 75% emergence, respectively (Table 2.3). Using parameter estimates from logistic analysis of the emergence trap captures of a

second generation of *D. platura* in 2003 (Table 2), the DD requirements for 10, 25, 50, 75, and 95% emergence ranged from 460.2 to 875.8, with corresponding JD estimates from 182.8 to 213.2 (Table 2.3). Using parameter estimates from logistic analysis of trap captures of the overwintered population in 2004 (Table 2.2), the DD requirements for emergence ranged from 295.2 to 434.0, with corresponding JD estimates from 161.1 to 174.4 (Table 2.3). For the F_1 generation, DD requirements for emergence ranged from 593.4 to 1028.7, with corresponding JD estimates from 185.4 to 218.2 (Table 2.3).

Trap collections started later in the season in 2002 than in other years, and the first recorded population peak apparently represented the second generation of adults, based on results in 2003 and 2004 when trapping started earlier. Mean calculations of the logistic analysis for the three-year trapping period (2002-2004) indicated that emergence of 25 to 95% of the overwintered population ranged from 295.2 to 434.0 DD, or from JD 164.0 to 174.4 (Table 2.4).

Emergence of 10 to 95% of the F_1 generation of *D. platura* ranged from 526.8 to 952.8 DD, or from JD 184.1 to 218.3 (Table 2.4). DD accumulations between the logistic 50% DD of the two generations were 255.0 ± 74.2 and 639.9 ± 69.4 for soil base values. Using just the means, the between-generation accumulation was 385 DD, using 50% emergence as the peak measure point.

Parameter estimates resulting from logistic analysis of *D. radicum* in either sticky or emergence trap captures are given in Table 2.5. Using the parameter values, the DD requirements of *D. radicum* for 10, 25, 50, 75, and 95% emergence ranged from 251.6 to 443.0 in 2002, over JD ranging from 171.1 to 186.4 (Table 2.6). Based on emergence traps in 2003, DD requirements ranged from 227.1 to 410.8, over 160.8 to 178.1 JD.

Sticky trap parameter estimates from 2003 indicated DD requirements ranging from 98.2 to 410.7, over JD estimates of 145.4 to 178.3. For 2004 emergence trap data, parameter estimates yielded DD requirements of 278.6 to 604.4, over JD ranging from 158.9 to 187.2 (Tables 2.5, 2.6).

Using results derived from the logistic analysis of data collected over the three years of my study, estimated DD accumulations are 213.7 ± 39.9, 273.9 ± 46.5, 324.5 ± 46.8, 375.7 ± 46.2, and 467.2 ± 46.3 for 10, 25, 50, 75, and 95% emergence of *D. radicum*, respectively. Corresponding JD estimates are 159.1 ± 5.3, 165.7 ± 4.2, 170.1 ± 3.5, 175.6 ± 3.7, and 182.5 ± 2.5 (Table 2.7). By compiling the DD means from the three years (2002-2004), 345.8 ± 79.4 DD (overall mean, soil-derived) were required for peak flight. The logistic calculation for 50% emergence of the population was 324.5 ± 46.8 DD (Table 2.7). Similarly the overall mean for peak captures from the three years is 171.5 ± 6.0 JD, compared with 170.1 ± 3.5 JD for 50% population capture determined using logistic analysis.

2.5 Discussion

DD models can play important roles in integrated pest management by predicting insect developmental rate, and so facilitate accurate timing in the implementation of control activities. DD accumulations are currently used in control programs for several Diptera including apple maggot, *Rhagoletis pomonella* (Walsh) (Laing and Heraty, 1984), sugarbeet root maggot, *Tetanops myopaeformis* (Roder) (Whitfield, 1984), onion fly, *Delia antiqua* (Meigen) (Andoloro et al., 1984), seedcorn maggot, *D. platura* (Funderburk et al., 1984), and cabbage maggot, *D. radicum* (Wyman et al., 1977; Collier

and Finch, 1985; Finch, 1993; Jyoti et al., 2003). The DD models developed here indicate that periods of peak adult activity of *D. radicum* occurred after approximately 345.8 ± 79.4 DD (soil base 4°C mean over three years) compared to 324.5 ± 46.8 for 50% capture. Peak flight activity of *D. platura* occurred at 339.5 DD (soil base 3.9°C in 2004) compared to a 50% capture estimate over three years of 255.0 ± 74.2 DD for the overwintered generation. The F_1 generation was recorded at 639.9 ± 69.4 DD for 50% captures over three years. These observations provide important background knowledge needed for managing both pests in canola in the Northern Great Plains.

Several developmental threshold values have been reported for *D. radicum*, including 6.1°C (Eckenrode and Chapman, 1971; Wyman et al., 1977) and 5.0°C (Bracken, 1988), but the threshold cited most frequently is 4.0°C (Collier and Finch, 1985). Interestingly, Collier and Finch (1985) used linear regression to determine that 4.3°C was the extrapolated base temperature for development of *D. radicum*, but instead recommended using 4.0°C. This has caused some confusion in the literature, because some authors used 4.3°C for model development (e.g., Johnsen et al., 1997) and others used 4.0°C (e.g., Jyoti et al., 2003), yet all quoted the same source. Here I used 4.0°C as the *D. radicum* threshold based on the recommendation of Collier and Finch (1985).

DD accumulations required for development of *D. radicum* in central Alberta were similar, but not identical, to those reported in other regions. For example, using the logistic method for emergence trap data in 2003, 10, 25, 50, 75, and 95% emergence of *D. radicum* required 227.1, 267.6, 307.4, 346.7, and 410.8 DD, respectively in central Alberta (DD range for 10 to 95% emergence = 183.7). In England, Collier and Finch (1985) reported that *D. radicum* required 179 ± 8 DD for 50% emergence, and that a

further 60 to 170 DD elapsed before maximum adult activity occurred in host crops. Alberta *D. radicum* populations therefore required ca 128.4 more DD than those in central England. Logistic analysis of in-crop populations over three seasons resulted in 10, 25, 50, 75, and 95% DD estimates of 213.7 ± 39.9, 273.9 ± 46.5, 324.5 ± 46.8, 375.7 ± 46.2, and 467.3 ± 46.3 DD. By comparison, in eastern U.S.A. Jyoti et al. (2003) found that 10, 25, 50, 75, and 95% emergence occurred after 176.6 ± 3.8, 204.2 ± 2.3, 251.3 ± 3.5, 297.6 ± 30.4, and 390.9 ± 10.1 DD, respectively (DD range for 10 to 95% emergence = 214.3). In central Alberta approximately 73 more DD were required for 50% emergence than in eastern U.S.A. However, such differences are not surprising because microclimate, population genetics, and host quality can all affect developmental requirements of insects (Pitcairn et al., 1992). Nair and McEwen (1975) studied *D. radicum* phenology in rutabaga in Ontario and reported that inadequate moisture delayed establishment of larvae, and believed that this explained the lack of correlation between thermal units and flight peaks.

My results indicate that JD logistic calculations were much less variable than DD computations for predicting flight and emergence of *D. radicum* and *D. platura*. For example, the peak JD capture period and 50% population JD logistic calculations were very similar for *D. radicum*: 171.5 ± 6.0 and 170.1 ± 3.5, respectively. However, substantial variations between years were observed for both *D. radicum* and *D. platura* in the DD requirements for 50% field captures. In 2002, for example, we found that emergence of 50% of the *D. radicum* population corresponded to JD 175.1 and 310.2 DD. However, in 2003 timing of 50% field captures of *D. radicum* corresponded to JD 161.1 and 227.8 DD; in 2004, this occurred at JD 176.0 and 452.7 DD. Bracken (1988)

also found considerable variation in the DD requirements for 50% emergence of *D. radicum* over a four-year period in rutabaga (*B. napus*) crops in Manitoba, and proposed that even though DD summations could predict fly emergence and activity with reasonable accuracy, calendar date was comparable or better as a predictive tool. Our results validate this observation for canola in central Alberta, and indicate that the timing of 50% emergence of *D. radicum* and the first generation of *D. platura* populations would be approximately JD 170.1 ± 3.5 (19 June for most years) and 160 ± 4.3 (9 June for most years), respectively. This explains the observation by Sanborn et al. (1982) that *D. platura* adults are commonly observed in the spring before cabbage maggot adults.

The existence of two generations of *D. platura* has potential influence on the population dynamics of univoltine species like *D. radicum*. Both *D. platura* and *D. radicum* are known as hosts of the staphylinid predator-parasitoid *A. bilineata* (Klimaszewski, 1984), and both are hosts for the fungal pathogen, *Entomophthora muscae* (Cohn) (Klingen et al., 2000). A second infusion of puparia into agricultural soil that can serve as additional hosts for *A. bilineata* can increase overwintering populations of the beetle, and could therefore enhance the impact of this natural enemy on populations of *D. radicum* in subsequent years. Similarly, a second generation of *D. platura* could produce an influx to the system of *E. muscae* and increase soil populations of overwintering fungal spores, perhaps increasing mortality to both species in subsequent generations.

I found no evidence of distinct early- and late-emerging populations within the same generation of *D. radicum*; instead, emergence trap captures indicated a single emergence peak in mid May (Figure 2.4). By contrast, Finch et al. (1988) found two *D.*

radicum biotypes in northern European populations, comprising early- and late-emerging adults from the overwintered generation, with large variation in the percentages of each type comprising local populations. Similarly, Biron and Coderre (2002) identified early- and late-emerging phenotypes of *D. radicum* in eastern Canada. Substantial genetic variation commonly occurs among species with broad geographic ranges (Avise, 1994). Determining the extent of this variation within temperate North American populations of *D. radicum* warrants further investigation to resolve differences in the population structure because of potential effects on its developmental biology and pest status. This investigation could perhaps best be undertaken by comparative molecular genetic analyses of populations from different ecoregions.

In all three years, small numbers of *D. radicum* were captured in August, several weeks after peak emergence. This likely indicates a precocious F_1 generation and not a late-emerging population of the overwintered generation. In northwestern Alberta, Broatch (1993) observed two distinct adult flight periods but concluded that there was not enough time prior to the onset of winter for the second population to lay eggs that could develop through to overwintering puparia. In Manitoba, Bracken (1988) also reported an F_1 generation in rutabaga, with peak activity on 12 August ± 11.7 days and DD (base 5.0°C) of 981 ± 229.3.

Using the developmental threshold of 3.9°C for *D. platura* developed by Sanborn et al. (1982), Funderburk et al. (1984) reported thermal-unit accumulation from overwintered puparia to peak (50% capture) adult activity at 206 DD (soil base) when averaged over two consecutive years. Corresponding accumulations from this study are 255 ± 74.2 DD. Funderburk et al. (1984) reported that, on average, an additional 616 DD

were required for development of the F_1 generation. In the present study, the F_1 generation appeared at 526.8 ± 66.6 DD, or just 384.9 DD after the 50% flight of the overwintered generation. Development from egg to adult requires 376 DD based on the model of Sanborn et al. (1982). Adult to adult development required an additional 15.7 DD to allow for the preovipositional period by females (Strong and Apple, 1958). Thus, an adult-to-adult peak should require about 392 DD, which is very similar to the 384.9 DD period found in my study. The differences between studies may be due to trapping methods or genetic characteristics of the populations. Unlike the sticky cards used in this study, Funderburk et al. (1984) utilized cone traps. Broatch and Vernon (1997) compared sticky cards with bowl traps, and found that the cards attracted significantly more males of *D. platura* during nine of 10 trapping periods, and significantly more females in seven of 10 trapping periods. Different trapping methods can therefore influence how DD or population percentages are calculated. In addition, the study by Funderburk et al. (1984) was conducted in Iowa, U.S.A., and populations there may comprise a genetically distinct biotype from those I sampled in western Canada.

The method used to sample populations of *Delia* spp. can influence reporting of population dynamics, and can even lead to misinterpretations of species phenologies. Broatch (1993) compared the effectiveness of bowl and sticky traps and found that in three of four sample periods females of *D. radicum* were much more attracted to yellow sticky cards than to bowls; males were significantly more attracted to cards than bowls in two of the four periods. My approach of describing flight patterns from sticky trap captures, and the timing of adult eclosion from emergence trap collections, was designed to utilize the most effective tools for documenting timing of both flight and emergence;

however, some observations are difficult to explain. For example, I found that sticky card captures of males of both *D. radicum* and *D. platura* often exceeded numbers of females. Since male:female ratios of both species from emergence trap collections were approximately 1:1, it seems that either males were less attracted to the cards than females, or they tended to be less active fliers than females. These observations agree with results of Broatch and Vernon (1997) who reported four times more males than females of *D. platura* on yellow sticky cards during mid summer in Alberta's Peace River region.

To be useful in integrated management programs, predictive modeling of insect development must be relatively easy to use within a timeframe that allows for monitoring flexibility. Predicting population trends with logistic curves was shown by Jyoti et al. (2003) to be a good indicator of *D. radicum* population trends in cole crop systems in northeastern U.S.A., and my study indicated similar accuracy in canola in western Canada. The adjusted R^2 for both the emergence and sticky trap captures was 99% in 2003 (Table 2.5). This phenological information will be extremely useful for facilitating accurate timing when an understanding of the population dynamics of *D. radicum* and *D. platura* is required for implementing control options, including biological control activities like augmentive or inoculative options.

This research provides insight into the population dynamics of two economically important root maggot species, and consequently my results have important implications for improved management of these pests in canola production in western Canada. JD is easier to determine and less variable for identifying peak flight and emergence than are DD calculations. In areas of western Canada where *D. radicum* and *D. platura* occur sympatrically, maximum flight activity of *D. platura* will occur in early June,

approximately two weeks before that of *D. radicum*. Primary damage to canola taproots by larvae of *D. radicum* seems to precede invasion by *D. platura*, which causes secondary damage. Emergence of *D. platura* before *D. radicum* could perhaps imply that *D. platura* attacks canola by causing primary feeding damage, but no evidence exists to confirm this and it is likely that *D. platura* either oviposits on alternate hosts early in the season or remains inactive reproductively until canola damage occurs. Because most oviposition by *Delia* spp. occurs on canola in the rosette to bud stages of development (Growth Stages 2.2 to 3.1 of Harper and Berkenkamp [1975]) (Griffiths, 1986a; Dosdall et al., 1994), growers should seed canola as early as possible in spring so plant development can be as advanced as possible by the time that peak flight of these species occurs. Plant compensation for root maggot attack is likely to be enhanced when canola is more developmentally advanced. Clayton et al. (2004) recommended seeding canola as soon as possible in spring for optimal yields; this recommendation is appropriate when considering results of the current study. My study also indicates that phenological determinations for the timing of peak periods of activity should be done on a regional basis. Although my results agree generally with those of other research, differences in DD and JD requirements occurred between *D. platura* and *D. radicum* in central Alberta and those from geographically distant populations. Species dynamics should therefore be considered over a wide range of environmental, ecological, and genetic influences. My research also emphasizes that sampling techniques and reporting methods should be standardized so that comparisons among species and populations can be meaningful and analogous.

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Table 2.1: Mean monthly temperature and precipitation data during the growing season at Lacombe, AB in 2002 to 2004 compared with long term average values.

	Mean monthly temperature (°C)				Mean monthly precipitation (mm)			
Month	2002	2003	2004	1908-2005 Mean	2002	2003	2004	1908-2005 Mean
April	-0.9	3.7	5.5	3.7	42.6	52.6	21.6	25.7
May	7.6	8.7	7.9	9.8	37.7	62.6	63.7	50.1
June	15.0	14.2	13.0	13.6	12.2	52.2	60.5	82.3
July	17.3	16.9	15.9	16.1	35.8	12.8	87.7	78.4
August	13.7	17.1	14.2	14.9	66.0	42.1	73.9	64.8
September	9.1	10.0	9.2	10.1	39.7	38.1	27.8	41.4
October	0.6	6.2	2.7	4.5	13.7	16.4	19.7	19.8

Table 2.2: Ordinary Least Squares parameter estimates resulting from logistic analysis of *Delia platura* adults from either sticky or emergence trap collections during 2002-2004.

Year/generation	Logistic model parameters[a]	Degree-days (± S.E.) (soil base 4°C)	Julian Date (± S.E.)
2002 (overwintered generation)	*a*	3.86 (7.55)	2.92 (5.88)
	c	97.64 (10.89)	97.96 (8.99)
	b	0.02 (0.01)	0.25 (0.07)
	m	524.57 (20.22)	192.34 (1.21)
	adjusted R^2	0.97	0.98
2003 (F_1 generation)	*a*	3.74 (6.63)	2.42 (5.02)
	c	101.57 (8.00)	100.85 (6.27)
	b	0.01 (0.00)	0.17 (0.03)
	m	602.76 (15.40	194.05 (0.92)
	adjusted R^2	0.99	0.99
2004 (overwintered generation)	*a*	-10.54 (4.41)	-11.05 (4.29)
	c	85.64 (6.22)	85.41 (6.27)
	b	0.04 (0.01)	0.43 (0.11)
	m	332.93 (7.07)	164.92 (0.71)
	adjusted R^2	0.98	0.99
2004 (F_1 generation)	*a*	100.50 (669.1)	18.64 (69.02)
	c	237.32 (787.8)	133.65 (90.79)
	b	0.004 (0.01)	0.09 (0.07)
	m	629.14 (1192.1)	199.43 (9.18)
	adjusted R^2	0.96	0.97

[a] *b* is the slope, *m* is the point of inflexion, *c* and *a* are asymptote parameters (equation 2.2)

Table 2.3: Estimates for degree-day and Julian day requirements for 10, 25, 50, 75, and 95% emergence of *Delia platura* adults based on logistic analysis of field trap collections of adults during 2002 to 2004.

Year/generation	% Emergence	Degree-days (soil base 3.9°C)	Julian date
2002 (considered F_1 generation)	10	N/A[a]	N/A[a]
	25	475.6	188.7
	50	536.3	193.0
	75	605.4	197.8
	95	N/A	223.4
2003[b] (overwintered generation)	10	N/A	N/A
(not a logistic analysis)	18.6	118.4	149.0
	50.2	180.8	156.0
	74.8	244.6	163.0
	95	N/A	N/A
2003 (F_1 generation)	10	460.2	182.8
	25	531.3	188.4
	50	611.7	194.5
	75	697.9	200.9
	95	875.8	213.2
2004 (overwintered generation)	10	N/A[a]	N/A[a]
	25	295.2	161.1
	50	329.2	164.5
	75	359.3	167.5
	95	434.0	174.4
2004 (F_1 generation)	10	593.4	185.4
	25	659.0	191.6
	50	771.7	200.0
	75	899.5	208.6
	95	1028.7	218.2

[a] N/A: estimation of degree-days or Julian days was not possible

[b] logistic analysis of the percent emergence of the 2003 overwintered generation could not be calculated due to limited data; values of 18.6, 50.2, and 74.8% emergence are based on actual field collections.

Table 2.4: Mean degree-day and Julian day requirements for 10, 25, 50, 75, and 95% emergence of *Delia platura* adults based on logistic analysis and peak capture period of overwintered and F_1 populations during 2002-2004.

Generation	% Emergence	Mean degree-days (± S.E.)	Mean Julian days (± S.E.)
Overwintered	10	—	—
	25	295.2 (N/A)*	164.0 (N/A)
	50	255.0 (74.2)	160.3 (4.3)
	75	301.9 (57.3)	165.2 (2.2)
	95	434.0 (N/A)	174.4 (N/A)
	Peak emergence	339.5 (N/A)	165.5 (N/A)
F_1 generation	10	526.8 (66.6)	184.1 (1.3)
	25	555.3 (54.3)	189.6 (1.0)
	50	639.9 (69.4)	195.8 (2.1)
	75	734.3 (86.8)	202.4 (3.2)
	95	952.8 (77.0)	218.3 (2.9)
	Peak emergence	594.5 (38.9)	191.7 (0.4)

* means with S.E. values given as N/A were based on a single year of data only; remaining means were based on 2-3 years of data

Table 2.5: Ordinary Least Squares parameter estimates resulting from logistic analysis of *Delia radicum* adults from sticky or emergence trap collections during 2002 to 2004.

Year/generation	Logistic Model Parameters[a]	Degree-days (± S.E.) (soil base 4°C)	Julian Date (± S.E.)
2002	*a*	26.51 (28.48)	67.30 (63.36)
(overwintered generation)	*c*	125.23 (28.58)	166.08 (63.48)
	b	0.02 (0.00)	0.26 (0.04)
	m	290.42 (23.31)	171.68 (2.90)
	adjusted R^2	0.99	0.99
2003	*a*	0.45 (0.82)	0.57 (0.78)
(overwintered generation)	*c*	99.99 (1.00)	99.74 (0.96)
(emergence trap)	*b*	0.03 (0.00)	0.30 (0.01)
	m	308.04 (1.98)	168.38 (0.17)
	adjusted R^2	0.99	0.99
2003	*a*	0.13 (7.62)	-5.36 (3.72)
(overwintered generation)	*c*	99.36 (7.93)	93.89 (3.93)
	b	0.02 (0.00)	0.18 (0.02)
	m	226.74 (12.3)	161.63 (0.65)
	adjusted R^2	0.99	0.99
2004	*a*	-8.11 (2.74)	-9.49 (2.75)
(overwintered generation)	*c*	90.98 (3.79)	89.45 (3.92)
	b	0.02 (0.00)	0.29 (0.05)
	m	460.15 (8.77)	176.62 (0.73)
	adjusted R^2	0.99	0.98

[a] *b* is the slope, *m* is the point of inflexion, *c* and *a* are asymptote parameters (equation 2.2)

Table 2.6: Estimates for degree-day and Julian day requirements for 10, 25, 50, 75, and 95% emergence of *Delia radicum* adults based on logistic analysis of sticky and emergence trap collections of adults during 2002- 2004.

Year/generation	% Emergence	Degree-days (soil base 4°C)	Julian Date
2002	10	251.6	171.1
(overwintered generation)	25	274.7	172.6
	50	310.2	175.1
	75	354.1	178.7
	95	443.0	186.4
2003	10	227.1	160.8
(overwintered generation)	25	267.6	164.6
(emergence trap)	50	307.4	168.3
	75	346.7	172.0
	95	410.8	178.1
2003	10	98.2	145.4
(overwintered generation)	25	162.7	154.3
	50	227.8	161.1
	75	293.6	167.4
	95	410.7	178.3
2004	10	278.6	158.9
(overwintered generation)	25	390.4	171.2
	50	452.7	176.0
	75	508.3	180.1
	95	604.4	187.2

Table 2.7: Mean degree-day and Julian day requirements (± S.E.) for 10, 25, 50, 75, and 95% emergence of *Delia radicum* adults based on logistic analysis and peak capture periods for overwintered populations during 2002-2004.

Generation	% Emergence	Mean degree-days (± S.E.)	Mean Julian days (± S.E.)
Overwintered	10	213.7 (39.9)	159.1 (5.30
	25	273.9 (46.5)	165.7 (4.2)
	50	324.5 (46.8)	170.1 (3.5)
	75	375.7 (46.3)	175.6 (3.7)
	95	467.2 (46.3)	182.5 (2.5)
	Peak emergence	345.8 (79.4)	171.5 (6.0)

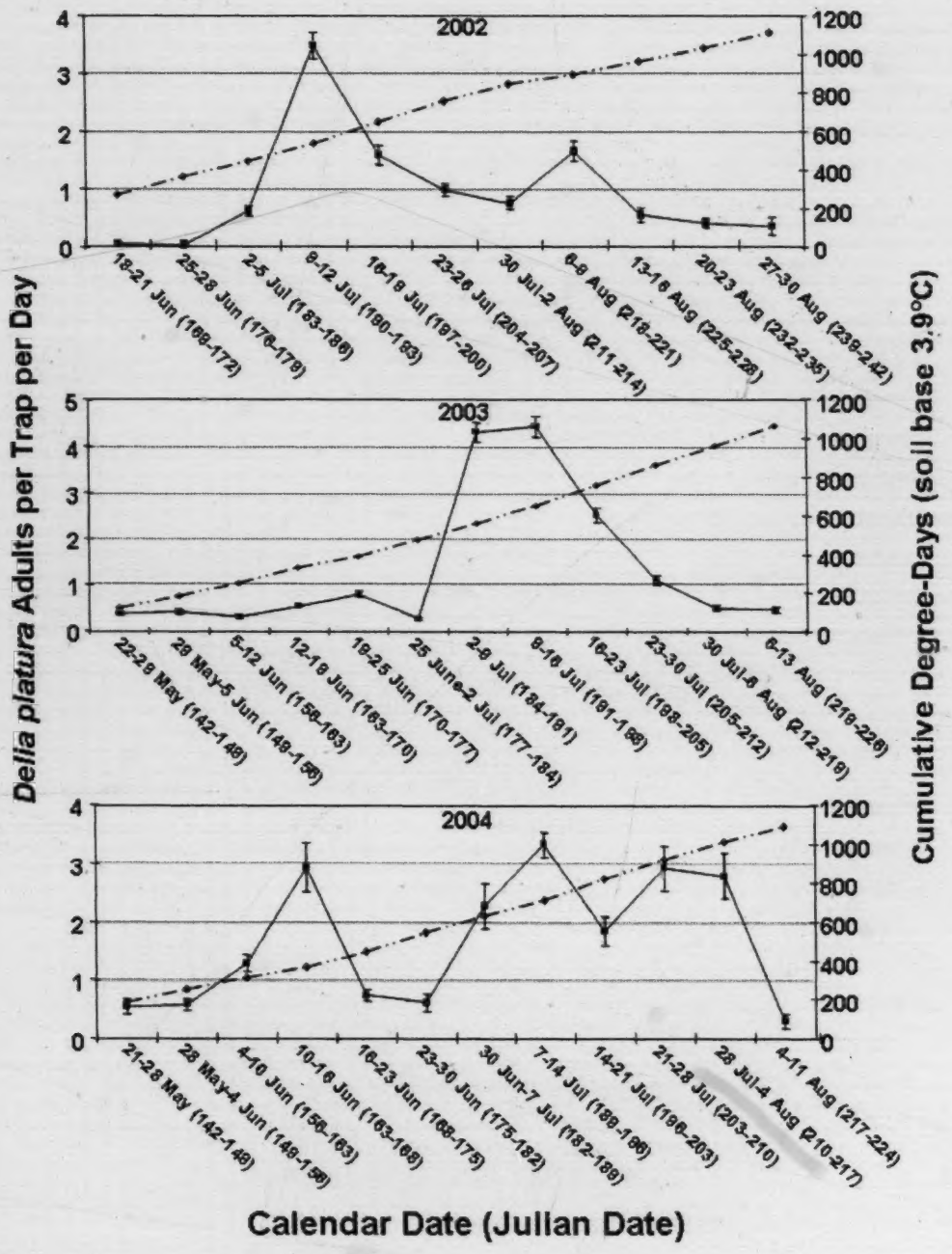

Figure 2.1: *Delia platura* adult captures per trap per day (± S.E.) on sticky traps in canola (solid line) compared with a 3.9°C soil developmental threshold requirement over three field seasons (2002-2004) (dashed line).

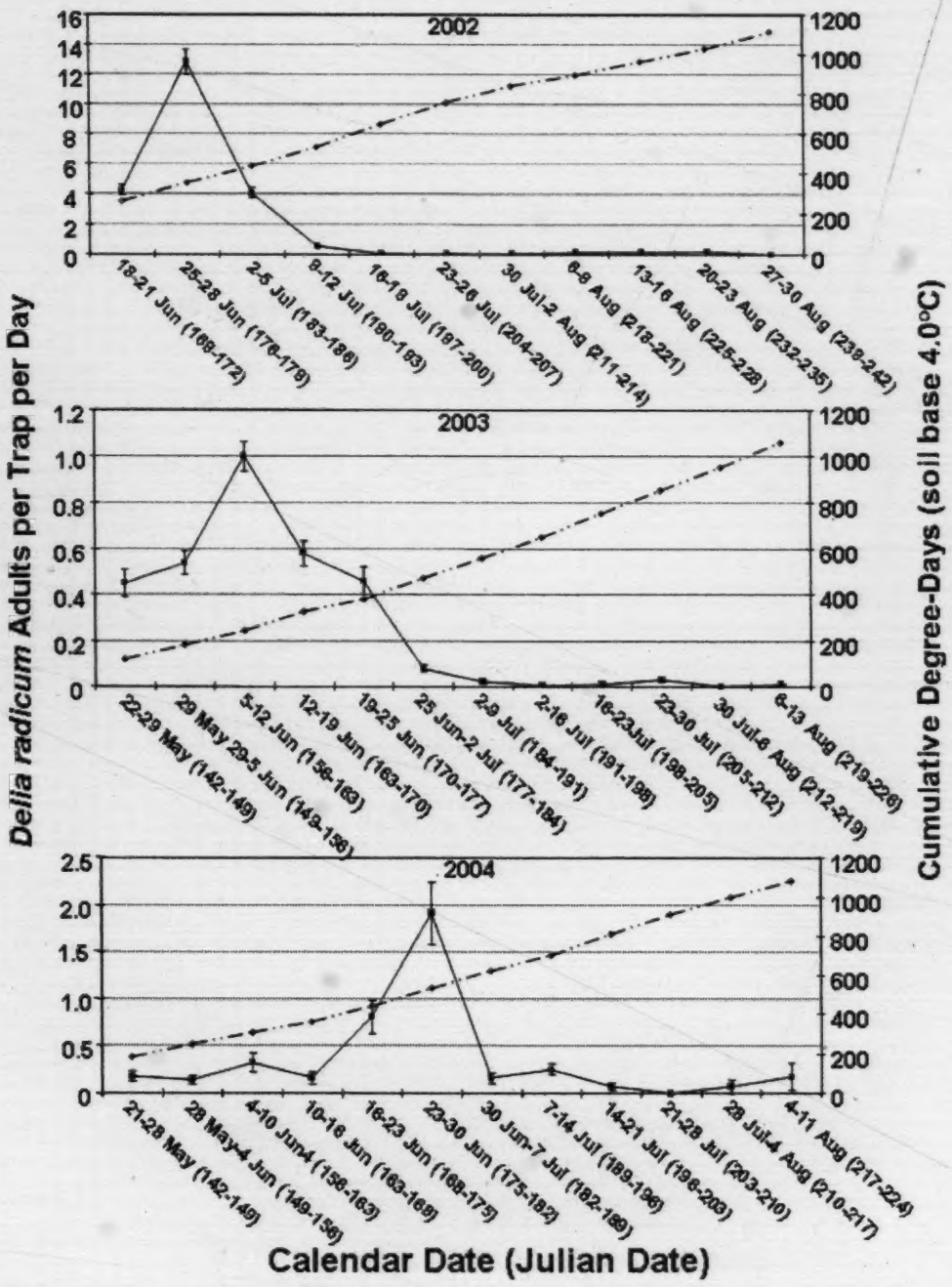

Figure 2.2: *Delia radicum* adult captures per trap per day (± S.E.) on sticky traps in canola (solid line) compared with a 4.0°C soil developmental threshold requirement over three field seasons (2002-2004) (dashed line).

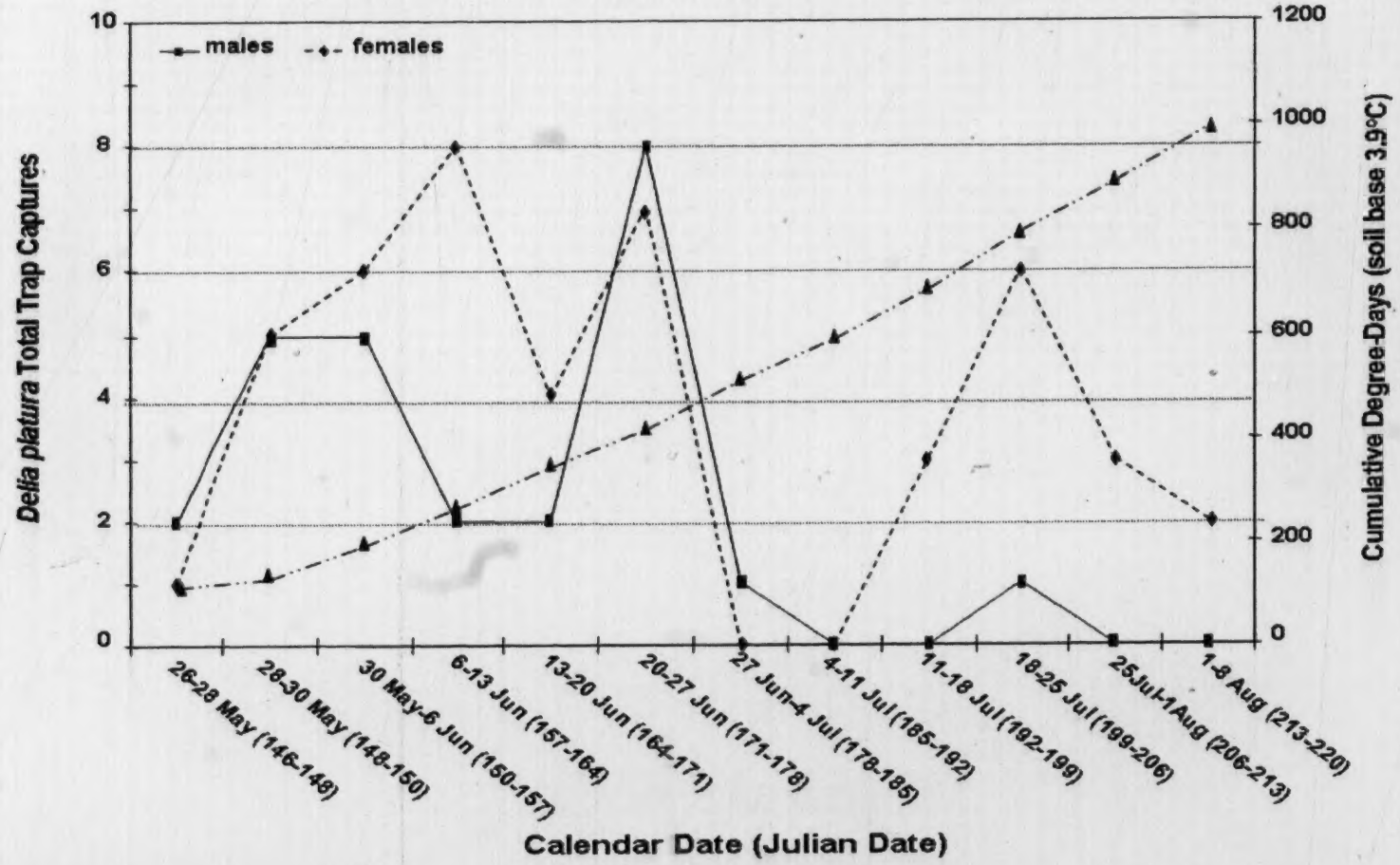

Figure 2.3: *Delia platura* adult captures from emergence traps on canola stubble compared with a 3.9°C soil developmental threshold requirement during 2003 (dashed line).

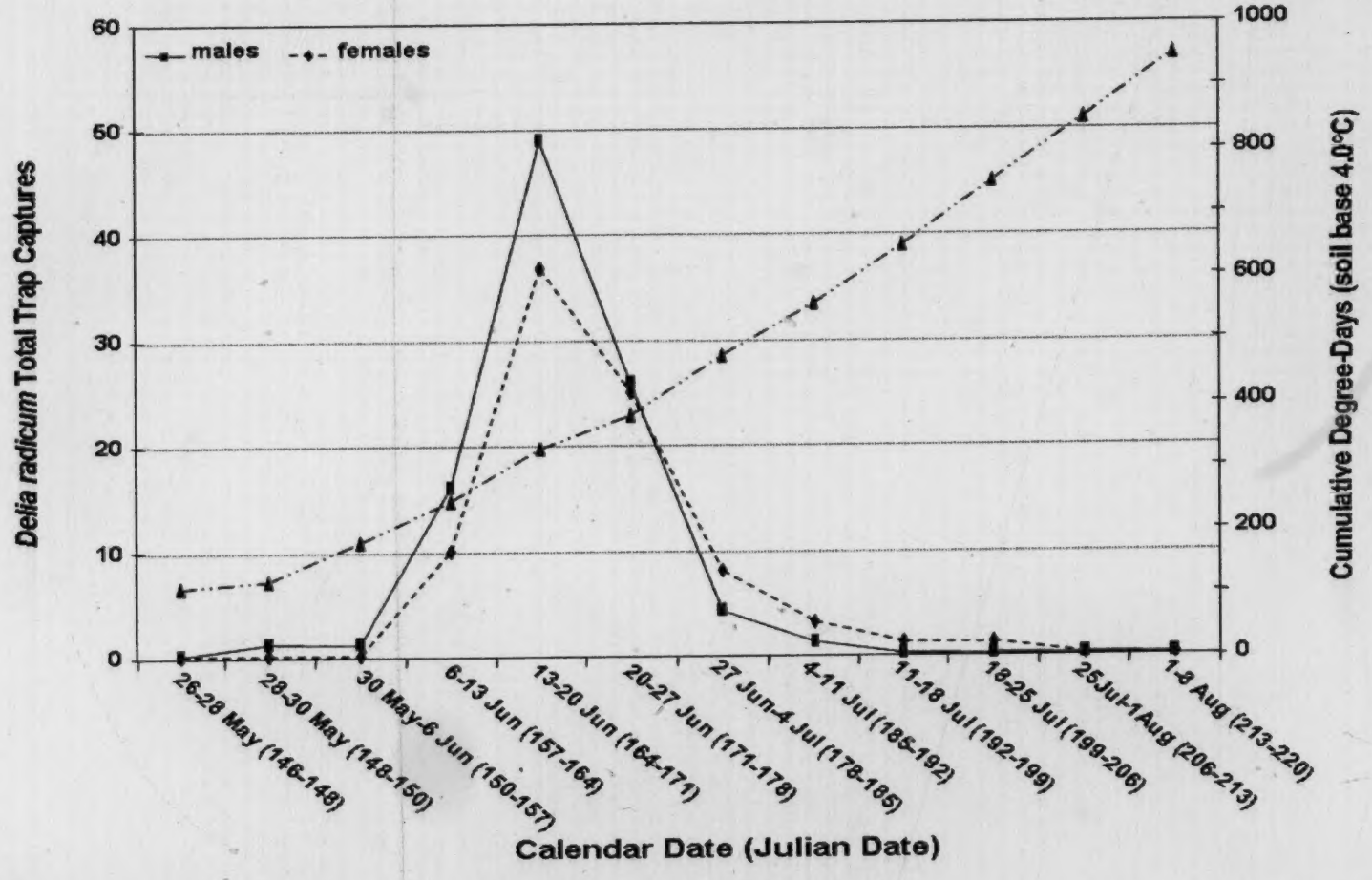

Figure 2.4: *Delia radicum* adult captures from emergence traps on canola stubble compared with a 4.0°C soil developmental threshold requirement during 2003 (dashed line).

Chapter 3: Herbicide Rate Effects on Weed and Root Maggot Dynamics in Canola[1]

[1] *Note*: A version of this chapter has been published:

Broatch, J.S., L.M. Dosdall, J.T. O'Donovan, K.N. Harker, and G.W. Clayton. 2008. Herbicide rate effects on weed and root maggot dynamics in canola. *Weed Science* 56: 477-483.

3.1 Abstract

Weed management strategies can influence insect infestations in field crops, yet no attempts have been made previously to manipulate weed populations in canola for integrated weed and insect management. Field studies were conducted during 2003 to 2005 at Lacombe and Beaverlodge, AB, Canada to manipulate weed and root maggot, *Delia* spp. (Diptera: Anthomyiidae), interactions in canola. Densities of monocot weeds were varied by altering herbicide (sethoxydim) applications, with rates ranging from 0 to 100% of the rate recommended. Weed populations declined, and yields were variable, with increases in herbicide rates. Root maggot damage decreased significantly ($P < 0.01$) with increases in monocot weed dry weights for both canola species at both study sites. Results support the hypothesis that heterogenous environments, arising from mixed populations of monocot weeds with canola, minimize opportunities for females of *Delia* spp. to complete the behavioral sequence required for oviposition, leading to reduced infestation levels in weedy systems. However, effects of dicot weeds on root maggot infestations varied between sites as a result of site-related differences in weed species complexes. When wild mustard (*Sinapis arvensis* L.) was common, crop damage increased, as this weed can serve as an alternate host for root maggots. The study

emphasizes the importance of adopting crop management practices that are compatible for both weed and root maggot control.

3.2 Introduction

Increasing biodiversity in annual crops has the potential for reducing the densities and economic impacts of herbivore pests (Altieri and Letourneau, 1984). Perhaps the simplest method for increasing plant biodiversity in annual crops is to tolerate a low density of weeds (Marshall et al., 2003). Although insect pests and weeds can interact, strategies aimed at managing either pest rarely consider such interactions. Weeds are regarded primarily as competitors of crop plants, and therefore the cause of subsequent yield reductions. However, O'Donovan (1992) demonstrated that late-emerging weeds usually have little or no impact on crop yield and their contribution to the weed seed bank is often insignificant. Weeds have been found to influence insect pest populations and their natural enemies in several crops such as winter wheat (*Triticum aestivum* L.) (Speight and Lawton, 1976), cotton (*Gossypium hirsutum* L.) (Showler and Greenberg, 2003), soybeans (*Glycine max* (L.) Merr.) (Buckelew et al., 2000), corn (*Zea mays* L.) (Pavuk and Stinner, 1991; Hough-Goldstein, 2004), and members of the Brassicaceae including Brussels sprouts (*Brassica oleracea* L., gemmifera group) (Smith, 1976), and collards (*B. oleracea*, acephala group) (Horn, 1988a, 1988b). A review of the interactions between weeds, arthropod pests, and their natural enemies in managed ecosystems determined that weed-insect pest interactions could be either negative or positive (Norris and Kogan, 2000).

In the Northern Great Plains of North America, canola (*Brassica napus* L. and *Brassica rapa* L.) is routinely grown in systems that strive to produce weed-free monocultures (Thomas, 2002), and the recent widespread adoption of herbicide-tolerant cultivars has enabled growers to manage weeds very effectively (Harker et al., 2000). A cornerstone weed management strategy in canola is to remove weeds early in crop development to minimize interspecific crop-weed competition for nutrients, water, and light (O'Donovan, 1992). However, recent research by Dosdall et al. (2003) found that infestations of root maggots (*Delia* spp.) (Diptera: Anthomyiidae) were reduced when weed removal occurred at the six-leaf stage of canola development compared with the two-leaf stage. Weedy backgrounds, or populations of weeds in densities sufficiently low that minimal interspecific crop competition occurred, seemed to minimize opportunities for females of *Delia* spp. to complete the behavioral sequence required for oviposition, leading to reduced root maggot infestations when weeds were removed later in crop development. Similar interactions between non-crop flora and root maggots have been reported in cabbage (*B. oleracea* L.) (Finch, 1996) and rutabaga (*B. napus* var. napobrassica) (Dixon et al., 2004).

Crop damage by *Delia* spp. occurs in canola when larvae feed on taproots, disrupting the flow of water and nutrients from the soil. Although several root maggot species can occur in canola, most damage is caused by the cabbage maggot, *Delia radicum* (L.), the turnip maggot, *Delia floralis* (Fallén), and the seed-corn maggot, *Delia platura* (Meigen) (Liu and Butts, 1982; Griffiths, 1986a, 1986b; Broatch et al., 2006). In recent surveys, root maggot damage occurred in 96% of commercial canola fields in Manitoba and Saskatchewan and 99.8% of fields in Alberta (Soroka et al., 2004). Yield

losses to *B. napus* from root maggot attack can range from 9 to 20%, with estimated yield losses as high as $100 million (Can.) annually (Griffiths, 1991; Soroka et al., 2004).

Improved understanding of the relationships that exist among crop plants, weeds, and insect herbivores may be exploited by producers for improved integrated crop management. Herbicide applications can enable manipulation of weed populations to achieve densities that do not compete excessively with crop plants for resources. At the same time, weeds may help reduce infestation levels of some herbivorous insects like root maggots. The objectives of this study were to investigate effects of different herbicide application rates on weed biomass, weed and root maggot infestation levels, and canola yield. We hypothesize that a low density of weeds could be maintained in canola without compromising yield, and could lower crop damage caused by root maggots. Such interactions have never previously been investigated in canola agroecoystems, yet they can lead to refinement of cropping strategies that promote the sustainability of canola agroecosystems.

3.3 Materials and Methods

3.3.1 Study Sites and Experimental Design

The study was conducted at the Agriculture and Agri-Food Canada Research Stations at Lacombe (113°44′W; 52°28′N) and Beaverlodge, AB (119°26′W; 55°13′N) during the 2003 to 2005 growing seasons. Soil types were Black Chernozem (Typic Haplustoll) with a neutral pH and 8 to 11% organic matter at Lacombe, and Dark Grey Solod (Molic Cryoboralf) with slightly acidic to neutral pH and an organic matter content of 4 to 6% at Beaverlodge.

The experiment was a randomized complete block design with four replicates. Twelve treatments were used, comprising one untreated control and five herbicide application rates for each of *B. rapa* and *B. napus*. Herbicide application rates comprised sethoxydim (Poast Ultra) applied at 20, 40, 60, 80, and 100% of the label rate of 200 g a.i. ha^{-1} in 2003, and 5, 10, 20, 40, and 100% of the label rate in 2004 and 2005, when canola was in the two- to three-leaf stage of development. Herbicides were applied in 110 L ha^{-1} of water at 275 kPa, using a sprayer equipped with flat-fan nozzles. Rainfall was monitored and recorded at each site during the period from seeding to harvest using tipping bucket rain gauges.

Prior to seeding, both sites were treated with glyphosate (Roundup WeatherMax®) at 540 g a.i. ha^{-1}. Plots of *B. napus* cv. InVigor 2733 and *B. rapa* cv. Hysyn 110 were seeded at Lacombe on 2 May 2003, 17 May 2004, and 10 May 2005, and at Beaverlodge on 2 May 2003, 17 May 2004, and 15 May 2005. Plots were seeded into cereal silage (*Hordeum vulgare* L.) stubble with a Conserva Pak® drill with 30.5 cm row spacings at a density of 150 seeds m^{-2}. Seed was treated with Helix® (containing 10.3% thiamethoxam, 1.24% difenoconazole, 0.39% metalaxyl-M, and 0.135 fludioxonil) at the manufacturer's recommended rate to reduce herbivory to seedlings by flea beetles (*Phyllotreta* spp.) (Coleoptera: Chrysomelidae). Plot dimensions were 8 by 15 m at Lacombe and 4 by 15 m at Beaverlodge, and soil was fertilized at 100% of the soil test recommendations for canola production. To simulate natural weed populations and to endeavor to obtain consistent population densities, tame oat (*Avena sativa* L.) was seeded at 100 seeds m^{-2} perpendicular to the canola seed rows. Applications of ethametsulfuron-methyl (Muster®) and clopyralid (Lontrel®) were applied in-crop at 22 g a.i. ha^{-1} and 150

g a.i. ha^{-1}, respectively, to control broad-leaved weeds. The herbicide applications (Poast Ultra®, Muster®, and Lontrel®) were made on 4 June 2003, 8 June 2004, and 9 to 10 June 2005.

3.3.2 Pre-harvest Weed and Crop Data

The following agronomic data were collected prior to harvest: crop emergence dates, weed emergence dates, flowering and maturity dates, and dry matter weights for both dicot and monocot weeds. Crop emergence dates were recorded approximately 10 d after seeding when seeded rows were clearly visible on the plots. Crop densities were determined by performing counts of seedlings approximately three weeks after emergence in 1-m strips for each of two rows at each of four randomly selected locations within each plot. Plot edges were not utilized in the sampling. Maturity date was determined as the time when 50% of the seeds in the pods on the lower racemes had turned brown.

Weed densities were determined for each plot approximately 48 h before and 20 d after the sethoxydim applications. All weed counts were obtained from four 0.5 m^2 quadrats positioned diagonally across each plot. Population counts (plants m^{-2}) of monocot and dicot weeds were conducted concurrently, with weeds identified to species and their growth stages recorded. Biomass of monocot and dicot weeds (kg ha^{-1}) was determined four weeks after spraying from within the same four quadrats where the original pre-spray counts were performed. Weeds were cut off at the root-stem interface, sorted by type (monocot or dicot), bagged, labeled, and dried at 60°C for 2 d before being weighed.

3.3.3 Yield and Dockage

At the end of the season, plots were swathed at 50% seed color change (Thomas, 2002), and plants remained in the swaths until drying to 10% moisture. Swaths were harvested using a John Deere 6620® modified plot combine, and yield data were recorded for each plot.

Harvested grain from each plot was dried to constant moisture and weighed. Grain was then subsampled (1000 g), and 500 g were passed over a Clipper® cleaning device with a 7/64 round screen on top and a 1/20 round screen on the bottom. Each sample was hand-cleaned of foreign material. The combined weight of the material separated from the subsample was used to calculate dockage as a percent of the 500 g subsample. The cleaned sample was then weighed and reported as the yield component.

Additional data collected for the study on yield and quality parameters are provided in Appendix 2.

3.3.4 Root Maggot Infestation Data

At harvest, a sample of 25 canola roots was collected randomly from each plot at each site. The roots were bagged and labeled, and returned to the laboratory and washed. Each root was then scored for degree of root maggot damage using the rating scale of Dosdall et al. (1994) where 0 = no root damage, 1 = less than 10% of the root surface with root maggot feeding channels, 2 = 11-25%, 3 = 26-50%, 4 = 51-75%, and 5 = 76-100% of the taproot surface area damaged.

3.3.5 Data Analyses

The relationship between herbicide rate and dry weights for each of the monocot and dicot weed components were investigated using nonlinear regression analysis (PROC NONLIN) (SAS 2004). The data were fitted to the model:

$$Y = \frac{K}{1 + E^{BG} X^{B}} + \mathrm{D} \qquad [3.1]$$

where Y is the estimated weed dry weight (kg ha^{-1}) and K, B, G, and D are estimated regression parameters, E is the base of the natural logarithm, and ED_{50} is the sethoxydim rate required to reduce weed dry weight by 50%.

The relationship between canola yield and sethoxydim rate was investigated by fitting data to the linear regression model:

$$Y = a + bX \qquad [3.2]$$

or

$$Y = a + bX + cX^2 \qquad [3.3]$$

where Y is the estimated canola yield, X is the sethoxydim application rate (percent of the recommended rate), a is the Y intercept, and b and c are estimated regression coefficients.

The relationship between root maggot damage and weed dry weight was investigated for each canola species using the linear regression model:

$$Y = a + b\mathrm{X} \qquad [3.4]$$

where Y is the estimated root maggot damage, a is the Y intercept, and b is the estimated regression coefficient. Weed dry weights data were transformed logarithmically, ln(x + 1), prior to analysis to stabilize variances in the samples and to meet the assumption of homoscedasticity for regression analysis. Weed dry weights within each site-year were

often clustered within a relatively narrow range of possible values. In order to span the widest possible range of values among weed dry weights, combined data for the three years of study were fitted to Equation 3.4 for each crop species and site.

Additional analyses performed on the data are described in Appendix 3.

3.4 Results and Discussion

3.4.1 Environmental Conditions and Plant Development

Precipitation at Lacombe during the 2003 growing season greatly exceeded long-term (1908 to 2005) normal values in April, but was substantially below average levels from June to August and in total growing season mean accumulations (Table 3.1). However, precipitation patterns during 2004 and 2005 were much closer to long-term mean values. Mean temperatures during 2003 to 2005 approximated long-term average values, although temperatures during August 2003 were warmer than average (Table 3.1).

Precipitation at Beaverlodge was substantially below long-term normal levels in May and July 2003, but above average in August (Table 3.1). In 2004, drier than average conditions occurred in May and June, but precipitation exceeded long-term normal levels in July, August, and September. In 2005, precipitation levels exceeded long-term average values for May through July. Mean temperatures at Beaverlodge approximated long-term average values during most of the growing seasons from 2003 to 2005 (Table 3.1).

At both study sites, environmental conditions and residual moisture levels from snow melt were favorable for germination of canola and weeds in each year of the study, but low precipitation in the summer of 2003 reduced crop yields at both sites. Root

maggot infestation levels are known to be correlated with soil moisture content (Griffiths, 1986b), and were reasonably high at each site and in each year of the study.

3.4.2 Weed Biomass in Response to Herbicide Rate

Weed populations were quite variable in different sites and years. For example, the monocot weed dry weights in untreated plots of *B. rapa* at Lacombe in 2004 were only 1.0% of those observed in 2003 (10.0 kg ha^{-1} in 2004 vs. 976.6 in 2003). Similar extremes occurred in Beaverlodge with maximum monocot dry weights in untreated plots of *B. napus* ranging from 126.3 kg ha^{-1} to 920.4 kg ha^{-1} in 2003 and 2005 respectively, representing a seven-fold variation in weed biomass. In addition to the tame oat seeded in our study to simulate monocot weed populations, low density populations of wild oat (*Avena fatua* L.), foxtail barley (*Hordeum jubatum* L.), and green foxtail (*Setaria viridis* (L.) Beauv.) also occurred in plots at both sites. The dominant dicot weeds showed greater site variability. At Lacombe, most dicot weeds were wild mustard, lamb's quarters (*Chenopodium album* L.), and dandelion (*Taraxacum officinale* G.H. Weber ex. Wiggers); at Beaverlodge, however, the dominant dicot weeds were wild buckwheat (*Polygonum convolvulus* L.), lamb's quarters, and common chickweed (*Stellaria media* (L.) Vill.). Herbicide applications for control of broadleaved weeds preceded root maggot oviposition by about 14 d. The broad-leaved herbicides destroyed most emergent target weeds, but weed emergence continued beyond the time when herbicides were applied, enabling some background weed populations to develop.

Monocot weed populations, as represented by their dry weights, were influenced by herbicide application rates at both study sites, with a decline in weed biomass as

herbicide rate increased (Figure 3.1). However, reductions in monocot weed biomass were not always proportional to the herbicide rate applied. For example, at Beaverlodge in 2003 weed biomass levels were similar among plots treated with herbicide at rates ranging from 20 to 100% of the label rate. As a consequence, herbicide application rates were altered during the 2004 and 2005 field seasons (from 20, 40, 60, 80, and 100% of the label rate in 2003 to 5, 10, 20, 40, and 100% of the label rate in 2004 and 2005), to achieve a broader range of background weed densities. Herbicide rate was responsible for most of the variation in weed biomass (Table 3.2; Figure 3.1). Relationships between weed dry weight and sethoxydim rate are presented graphically only for *B. napus* cv. InVigor 2733 at each site because results were similar for *B. rapa* cv. Hysyn 110. All equations were significant at $P < 0.001$. ED_{50} values increased from 2003 to 2005 and tended to be lower at Beaverlodge than at Lacombe (Table 3.2).

As expected, dockage values were associated with herbicide application rates. Highest dockage levels occurred in the untreated plots (ranging from 68% for *B. rapa* at Beaverlodge in 2005 to 22% for *B. napus* at Lacombe in 2005). Dockage levels were usually lowest in plots treated at 80 or 100% of the registered herbicide rate (ranging from 29% for *B. rapa* plots at Beaverlodge in 2003 to 2% for *B. napus* plots at Lacombe in 2004) (data in Appendices).

3.4.3 Seed Yield Responses to Herbicide Rate

High weed densities did not always correspond with yield losses for either canola species: for instance at Lacombe in 2003 weed populations were very high in plots subjected to the 0 and 20% herbicide rate treatments, yet this did not translate into

significant yield losses. The adjustment of herbicide rates in 2004 and 2005 to obtain a more gradual decline in weed populations with increasing herbicide rate was successful, but yield was not always affected significantly. Nevertheless, sethoxydim application rate did explain a substantial component of the variance in yield for *B. napus* in three site-years and for *B. rapa* in two site-years (Table 3.3).

3.4.4 Interactions Between Root Maggot Infestations and Herbicide Rate

Mean root maggot damage ratings were variable for canola species and year (Table 3.4). At Lacombe, mean damage ratings were greater for *B. rapa* than *B. napus*, and substantially greater in 2003 and 2004 than in 2005. At Beaverlodge, mean root maggot damage was similar for the canola species in 2003, but greater for *B. rapa* than *B. napus* in 2004 and 2005. Root damage at Beaverlodge in 2003 exceeded values observed in 2004 and 2005 (Table 3.4). Dosdall et al. (1994) also found susceptibility differences among canola species to root maggot infestations, with *B. rapa* more susceptible than *B. napus*. Mean root maggot damage values greater than 2.0 are usually associated with yield loss in the absence of weed infestations (Dosdall, 1998). In previous research, a yield decline of 192 kg ha^{-1} was observed for each unit increase in mean root maggot damage rating (Dosdall et al., 2004).

Root maggot damage decreased significantly ($P < 0.05$) with increases in monocot weed dry weight for both *B. napus* and *B. rapa* at Lacombe and Beaverlodge (Table 3.5; Figure 3.2). This relationship explained the greatest amount of sample variance for *B. napus* at Beaverlodge ($r^2 = 0.36$), and the least for *B. rapa* at Lacombe ($r^2 = 0.06$). Root maggot damage varied in its interactions with dicot weeds at Lacombe and

Beaverlodge (Table 3.5; Figure 3.3). At Lacombe, root maggot damage increased significantly ($P < 0.05$) as dicot weed dry weight increased, but at Beaverlodge damage from root maggots declined as dicot weed weight increased.

Results of this study agree with previous research by Dosdall et al. (2003) who reported that root maggot damage to canola was affected by background populations of weeds. Dosdall et al. (2003) found that root maggot damage declined with a delay in time of weed removal from the two- to the six-leaf stages of canola development: the longer weeds remained established in canola cropping systems, the less root maggot damage was inflicted. Several ecological hypotheses have been given in the literature to explain lower insect populations and their associated damage in heterogenous cropping systems (Altieri and Letourneau, 1984), and of these, the most applicable to interactions among canola, weeds, and root maggots seems to involve behavioural interference. Kostal and Finch (1994) found that mated, gravid females of *D. radicum* require an average of four spiral flights before ovipositing on a suitable host plant. During this process, a female lands on a suitable host plant, takes flight, lands again, and so on, until an average of four consecutive landings have occurred. An 'inappropriate landing' on a non-host plant like oats, can require the process to begin over again (Finch and Collier, 2000). Dosdall et al. (2003) proposed that such inappropriate landings resulted in less root maggot damage when canola was grown in weedy backgrounds. In canola cropping systems in western Canada, early weed removal is often recommended for optimal yields (Clayton et al., 2002; Martin et al., 2001; O'Donovan, 1992), but this practice can be associated with increased root maggot damage (Dosdall et al., 2003).

My results indicate that although increases in monocot weed populations were consistently associated with reductions in root maggot damage (Figure 3.2), this effect was variable for dicot weeds (Figure 3.3). The distinctive responses in root maggot damage to dicot weed dry weights at Lacombe and Beaverlodge were likely related to the differential species composition of dicot weeds at each site. At Lacombe, the dominant dicot weed species in two of the three site-years of study was wild mustard, a member of the Brassicaceae and an alternate host of the crucifer specialist, *D. radicum* (Finch and Ackley, 1977). At Beaverlodge the dominant dicot weeds (wild buckwheat, lamb's quarters, and common chickweed) were not alternate hosts for root maggots. Background populations of wild mustard at Lacombe may have served to increase overall root maggot infestation levels because of its susceptibility to infestation by these pests.

A relationship between canola yield and herbicide application rate occurred in three of six site-years of study. I found an increase in yield at higher herbicide application rates, even though root maggot damage was greater at these higher rates. Yield losses due to weeds can be influenced by crop genotype, weed phenology, and soil moisture and fertility levels (Liebman et al., 2001), and it seems that these effects were sufficiently important in this study to override any yield advantage gained by reduced root maggot attack at higher weed densities.

In some other cropping systems, weed species composition and their temporal and spatial dynamics were found to affect root maggot infestation levels, but these aspects remain to be clarified in canola agroecosystems. For example, O'Donnell and Coaker (1975) found that 60% soil cover by clover (*Trifolium* sp.) was needed in Brussels sprouts (*B. oleracea*) to reduce oviposition by *Delia* spp., and the differences in egg

numbers with and without appropriate clover cover were reflected in the root damage index. As well, Finch and Kienegger (1997) reported that clover must cover 50% of the vertical profile of the crop plants to have maximum influence on root maggot infestation levels, and a temporal aspect of plant growth during pest activity was important. In canola, therefore, the effectiveness of different weed species for reducing root maggot infestations, the timing of weed growth and development in relation to periods of *Delia* spp. flight and oviposition, and the degree of ground cover necessary for optimal root maggot control need to be determined to identify optimal integrated management practices for concurrent infestations of weeds and root maggots.

Altering crop monocultures through additions to weed biodiversity can influence humidity and light penetration in the crop canopy, as well as other aspects of the microclimate, such as the availability of protective refugia (Landis et al., 2005; Pavuk et al., 1997), and these in turn could influence the abundance of root maggot predator-parasitoids like *Aleochara bilineata* (Gyllenhal) (Coleoptera: Staphylinidae). This species is a voracious predator of root maggot eggs and larvae, with a single adult beetle capable of consuming an average of 23.8 eggs or 2.6 larvae per day (Read, 1962). Although effects on egg predation by *A. bilineata* were not assessed in this study, the possibility remains that protective refugia or altered microclimates generated by low densities of weeds in canola enabled *A. bilineata* populations to increase with concomitant losses of root maggot eggs. Refugia from low-density weed populations may also affect carabid beetle species that feed on weed seeds. For instance, Kromp (1989) found that carabid beetle numbers were higher in biologically managed fields due to their greater weediness and heterogeneity, and the absence of pesticides. Several

studies have associated higher ground beetle numbers with weedy situations (Norris and Kogan, 2000), but the effects of weedy backgrounds on natural enemies of insect pests and on insects that consume weed seeds are important relationships that remain to be investigated in canola cropping systems.

My study is the first of its kind to manipulate weed densities in canola cropping systems with the objective of achieving integrated management of both weeds and root maggots. Dewar et al. (2003) advocated a similar approach in sugar beet (*Beta vulgaris* L.) where genetically modified herbicide-tolerant cultivars were proposed as a platform for crop management to enhance weed and insect populations without compromising yield. This study demonstrated that while such creative applications of herbicide tolerant technology hold promise, the natural environmental variability associated with site and year makes it difficult to achieve fine adjustments to weed population densities. For example, applying herbicide at 40% of the label rate to herbicide-tolerant *B. napus* resulted in weed biomass levels ranging from 1.4 to 17.0 kg ha^{-1} at the Lacombe site over the three years of the study. Such a wide range in weed populations makes it difficult to predict and exploit the relationship that exists between weeds, root maggots, and yield for a given herbicide rate.

Results of this study emphasize the importance of adopting management practices that are compatible for both weed and root maggot control, as proposed by Dosdall et al. (2003). In a comprehensive review of integrated weed management approaches for spring-sown crops in western Canada, O'Donovan et al. (2007) proposed integrating reduced herbicide rates with agronomic practices that improve crop competitiveness over weeds because herbicides can sometimes perform more efficaciously in the presence of

crop competition. Reducing herbicide application rate may then be another compatible management strategy for both pests that has been inadequately exploited in canola cropping systems, especially when used in combination with competitive varieties.

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Table 3.1: Mean monthly temperature and precipitation data for the Lacombe and Beaverlodge, AB study sites for the 2003 to 2005 growing seasons in comparison with long-term average values (1908-2005).

		Mean precipitation (mm)				Mean temperature (°C)			
Site	Month	2003	2004	2005	1908-2005	2003	2004	2005	1908-2005
Lacombe	April	52.6	21.6	3.5	25.7	3.7	5.5	5.7	3.7
	May	62.6	63.7	22.6	50.1	8.7	7.9	10.3	9.8
	June	52.2	60.5	123.4	82.3	14.2	13.0	12.8	13.6
	July	12.8	87.7	49.6	78.4	16.9	15.9	15.6	16.1
	August	42.1	73.9	110.1	64.8	17.1	14.2	13.1	14.9
	September	38.1	27.8	59.5	41.4	10.0	9.2	8.8	10.1
	Total	260.4	335.2	368.7	342.7				
Beaverlodge	April	26.5	20.7	11.0	20.1	2.0	5.1	5.3	3.1
	May	14.4	14.8	64.0	38.1	8.4	8.2	10.9	9.5
	June	54.6	48.7	86.5	62.2	13.9	14.8	13.2	13.3
	July	43.3	95.6	78.8	64.6	16.3	16.4	13.9	15.4
	August	69.5	85.5	49.4	54.7	14.2	14.1	12.8	14.4
	September	34.0	123.0	24.8	43.0	9.5	7.8	8.6	9.8
	Total	242.3	378.3	314.5	282.7				

Table 3.2: Regression estimates and ED_{50} values for monocot weed dry weight as a function of sethoxydim application rate for *Brassica napus* and *Brassica rapa* at Lacombe and Beaverlodge, AB.

Location	Canola species	Year	Regression equation	r^2	ED_{50}
Lacombe	*B. napus*	2003	$Y = \frac{697}{1 + E^{-5.9} X^{2.4}}$	0.79	12
		2004	$Y = \frac{8}{1 + E^{-4.2} X^{1.5}}$	0.80	16
		2005	$Y = \frac{56}{1 + E^{-8.2} X^{2.3}}$	0.41	36
	B. rapa	2003	$Y = \frac{977}{1 + E^{-5.6} X^{2.4}}$	0.91	11
		2004	$Y = \frac{11}{1 + E^{-8.6} X^{2.6}}$	0.92	27
		2005	$Y = \frac{75}{1 + E^{-3.8} X^{1.1}}$	0.65	36
Beaverlodge	*B. napus*	2003	$Y = \frac{126}{1 + E^{-3.3} X^{0.98}}$	0.95	10
		2004	$Y = \frac{616}{1 + E^{-10.5} X^{3.9}}$	0.89	15
		2005	$Y = \frac{968}{1 + E^{-3.7} X^{1.5}}$	0.72	18
	B. rapa	2003	$Y = \frac{176}{1 + E^{0.67} X^{0.24}}$	0.86	0.1
		2004	$Y = \frac{732}{1 + E^{-0.37} X^{1.5}}$	0.90	13
		2005	$Y = \frac{1170}{1 + E^{-5.8} X^{1.8}}$	0.72	26

Table 3.3: Regression estimates for yield as a function of sethoxydim application rate for *Brassica napus* and *Brassica rapa* at Lacombe and Beaverlodge, AB.

Location	Year	Canola species	Regression estimates[a]			
			a	b	c	r^2
Lacombe	2003	*B. napus*				ns
	2004	*B. napus*	3270	3.9	—	0.32
	2005	*B. napus*				ns
	2003	*B. rapa*				ns
	2004	*B. rapa*	1799	5.6	—	0.72
	2005	*B. rapa*				ns
Beaverlodge	2003	*B. napus*	1039	1.7	—	0.31
	2004	*B. napus*				ns
	2005	*B. napus*	983	22.4	0.14	0.72
	2003	*B. rapa*				ns
	2004	*B. rapa*				ns
	2005	*B. rapa*	522	15.2	0.08	0.76

[a] Data were fitted to Equations 3.2 or 3.3 (see text). Regression estimates are not presented where results were not significant statistically ($P > 0.05$).

Table 3.4: Mean root maggot damage ratings and mean standard errors (S.E.) for *Brassica napus* and *Brassica rapa* at Lacombe and Beaverlodge, AB, 2003-2005.

Location	Year	Canola species	Root damage rating	
			Mean	S.E.
Lacombe	2003	*B. napus*	1.87	0.09
	2004	*B. napus*	1.94	0.11
	2005	*B. napus*	0.34	0.04
	2003	*B. rapa*	2.96	0.07
	2004	*B. rapa*	2.92	0.07
	2005	*B. rapa*	1.51	0.12
Beaverlodge	2003	*B. napus*	3.42	0.06
	2004	*B. napus*	1.27	0.09
	2005	*B. napus*	1.24	0.06
	2003	*B. rapa*	3.36	0.07
	2004	*B. rapa*	2.61	0.08
	2005	*B. rapa*	2.71	0.03

Table 3.5: Regression estimates for root maggot damage as a function of monocot and dicot weed dry weights recorded after herbicide application for *Brassica napus* and *Brassica rapa* at Lacombe and Beaverlodge, AB.

Location	Canola species	Regression estimates[a]		
		a	b	r^2
Monocot weeds:				
Lacombe	*B. napus*	1.9	-0.18	0.12
	B. rapa	2.8	-0.12	0.06
Beaverlodge	*B. napus*	3.9	-0.40	0.36
	B. rapa	3.5	-0.13	0.21
Dicot weeds:				
Lacombe	*B. napus*	1.2	0.18	0.14
	B. rapa	2.3	0.18	0.15
Beaverlodge	*B. napus*	2.9	-0.64	0.54
	B. rapa	3.1	-0.15	0.13

[a] Data were fitted to Equation 3.4 (see text). All regression equations were significant statistically ($P < 0.01$ except Lacombe, *B. rapa* monocot weed $P = 0.036$).

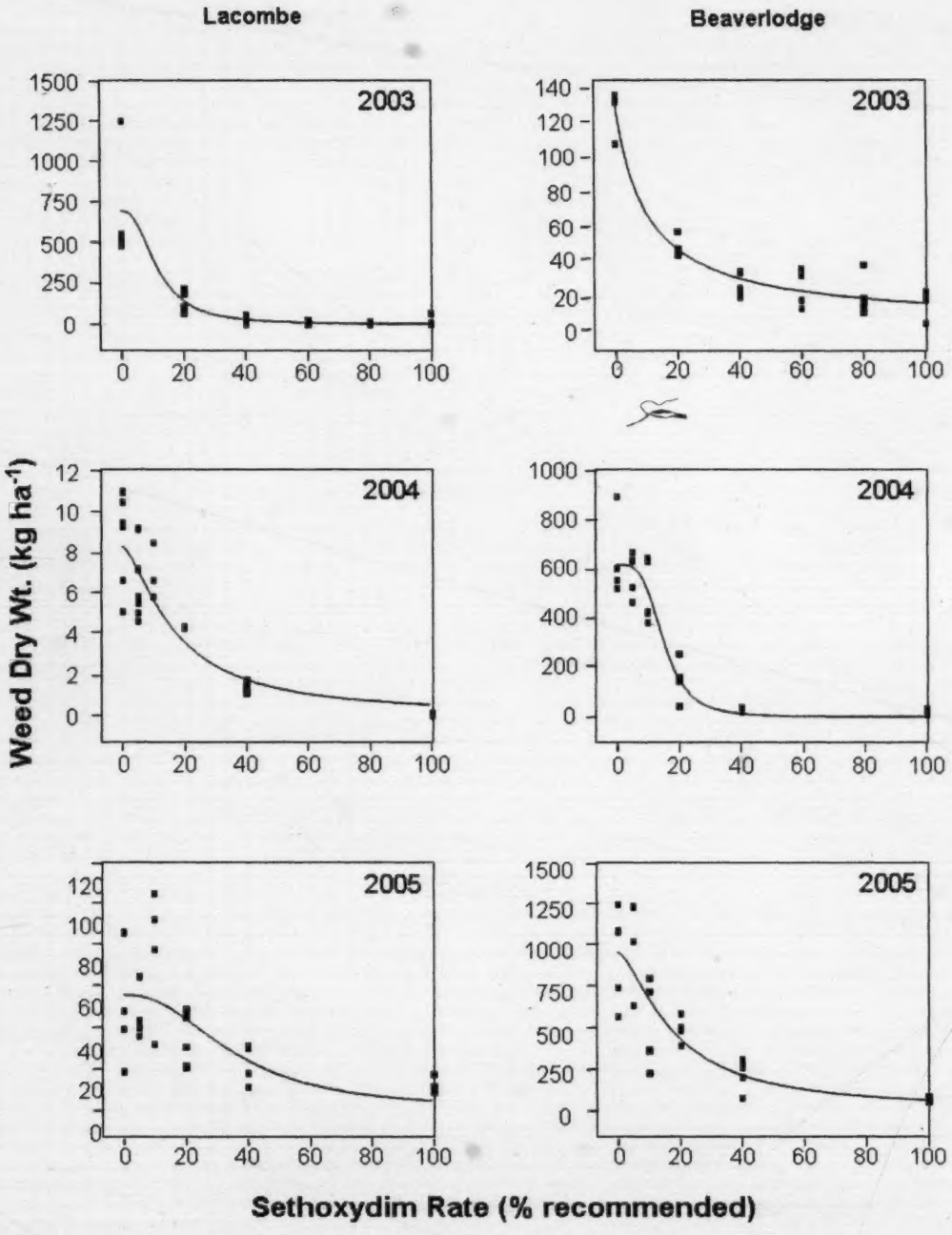

Figure 3.1: Responses of weed dry weight to application rate of sethoxydim herbicide in canola (*Brassica napus*) at the Lacombe and Beaverlodge, AB sites from 2003 to 2005. Data were fitted to Equation 3.1 (see text), and curves are based on regression estimates presented in Table 3.2.

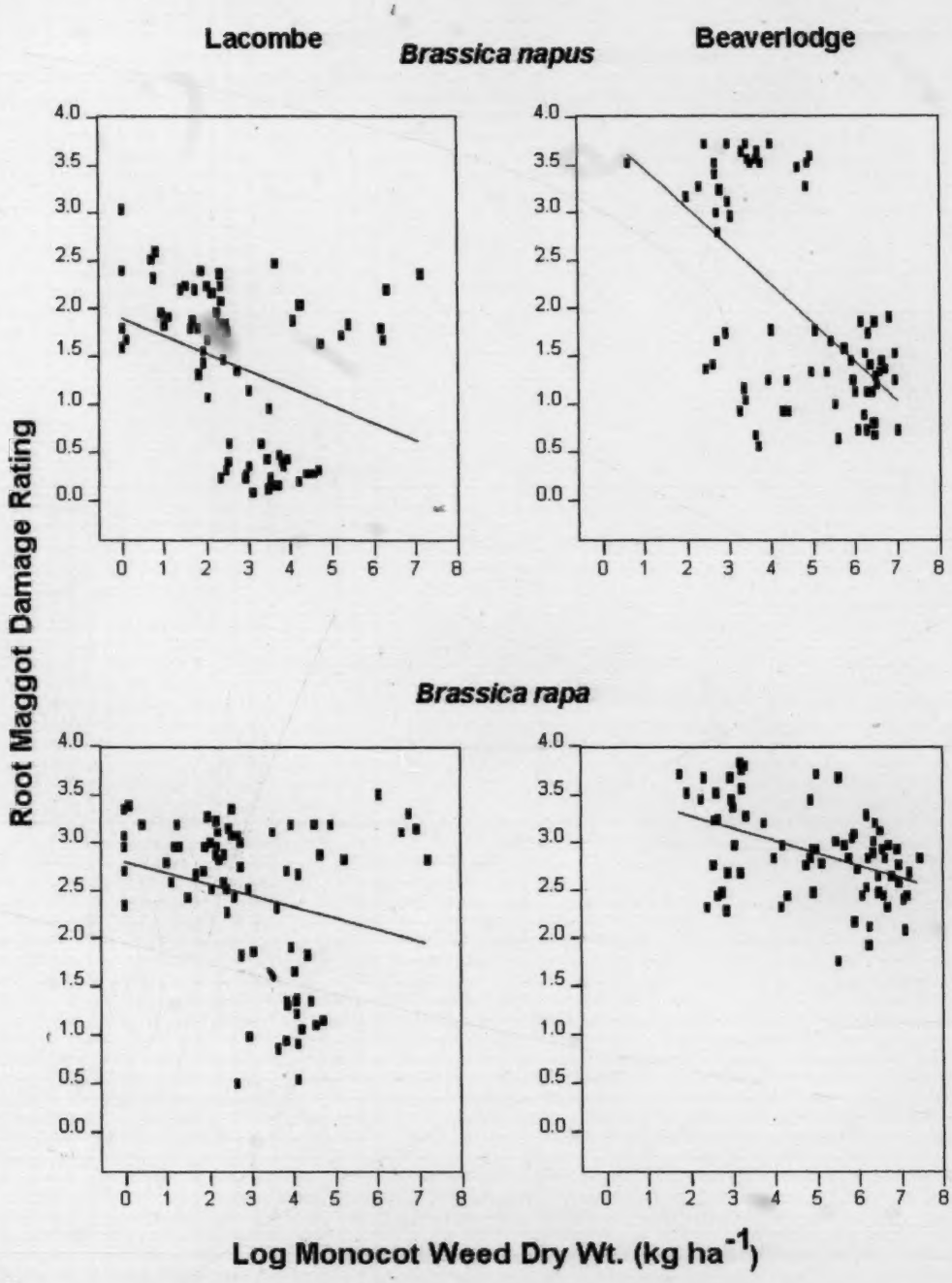

Figure 3.2: Responses of monocot weed dry weight to root maggot damage to taproots of *Brassica napus* and *Brassica rapa* at the Lacombe and Beaverlodge, AB sites using combined data for 2003 to 2005 inclusive. Data were fitted to Equation 3.4 (see text), and curves are based on regression estimates presented in Table 3.4.

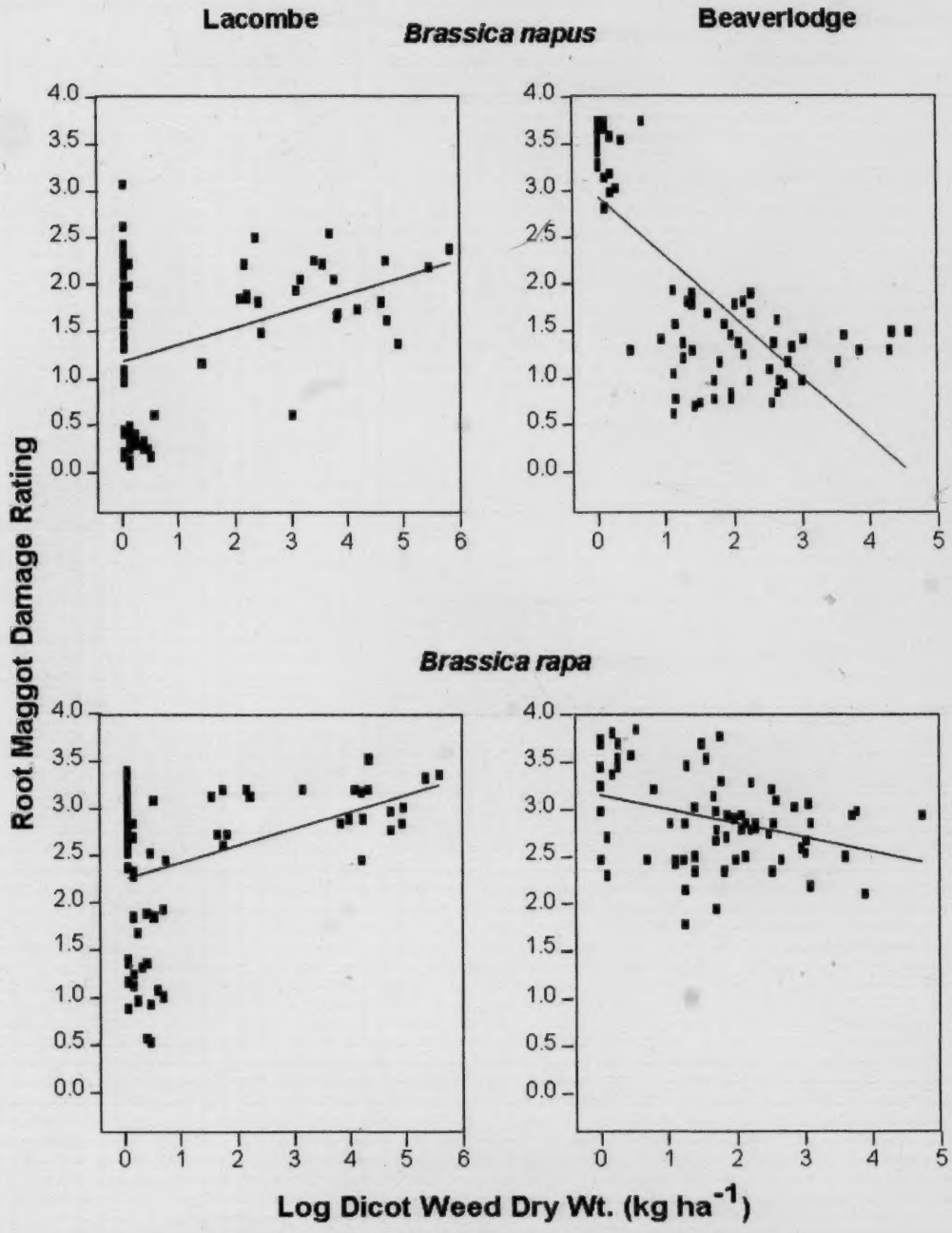

Figure 3.3: Responses of dicot weed dry weight to root maggot damage to taproots of *Brassica napus* and *Brassica rapa* at the Lacombe and Beaverlodge, AB sites using combined data for 2003 to 2005 inclusive. Data were fitted to Equation 3.4 (see text), and curves are based on regression estimates presented in Table 3.4.

Appendix: Chapter 3: Herbicide rate impacts on weed, root maggot damage and crop quality in canola

A3.1 Background

The research described in Chapter 3 documents some effects of herbicide application rate variations on various agronomic parameters (yield, dockage, weed biomass), and on infestations of root maggots (*Delia* spp.; Diptera: Anthomyiidae) in the canola research plots. However, additional data were collected as part of this study, for example to assess variations in crop quality associated with different herbicide rates, and data were subjected to analysis of variance using PROC MIXED of SAS (SAS Institute Inc., 2004) to further explore treatment effects. In addition, contrasts were designed for comparing herbicide effects on the different crop quality parameters.

The purpose of this appendix is to present these additional data, and to describe their analyses, and thereby provide a more complete representation of the total scope of the study, and to further explore results of the study.

A3.2 Materials and Methods

The experimental design and most aspects of agronomic components measured were described in Chapter 3. Here I provide additional descriptions of methods undertaken for this study.

A3.2.1 Root Maggot Oviposition Data

Root maggot egg densities were determined for three consecutive weeks during the peak period of oviposition from mid-June to early July of each season, 2003 to 2005. On each sampling date, the numbers of root maggot eggs deposited on 25 canola plants were counted from each plot. Plants growing in sequence from a randomly selected starting point in a predetermined row were examined *in situ* and the eggs laid at the base, the lower leaf axils, and in the soil in a 1-cm-radius and a 1-cm-depth around the plant stalks were counted and recorded according to the method of Dosdall et al. (1994).

A3.2.2 Yield and Crop Quality

After plots were swathed, threshed, and the grain cleaned of foreign material, thousand kernel seed weights were obtained from a random sample taken from the cleaned grain. Protein content was derived using Near-Infrared Reflectance Spectroscopy. Oil content was determined from 20 g of whole seeds from the clean sample with Nuclear Magnetic Resonance (NMR) utilizing a Newport Analyser Mk IIIA[12]. Samples were dried in coin envelopes for 48 h at 35°C, followed by cooling for 24 h at room temperature. Results of oil and protein analyses were reported as percentages of seed weight.

A3.2.3 Data Analyses

ANOVA was performed on all data sets using PROC MIXED (SAS Institute Inc. 2004). Mean and standard error measures as reported graphically were obtained from the output of the LSMEANS statement of PROC MIXED. Differences in monocot weed dry weights, thousand kernel weights, and percentages of protein, oil, and dockage were

determined for plots subjected to the different herbicide application rates using the option ADJUST=TUKEY in the LSMEANS statement of PROC MIXED. For monocot weed dry weights and percent dockage data log-transformation, $\log_{10}(x + 1)$, was required to reduce the coefficients of variation to an acceptable level of <30%. A further insight was gained, through the use of PROC REG, on the trend of responses to different herbicide application rates on all agronomic characters. With the six levels of herbicide application rates, it would be possible to fit a polynomial function of the fifth order. However, the final parsimony model would include the only regression coefficients that were significantly different from zero ($P < 0.05$).

Root maggot damage ratings were analyzed as a randomized complete block design with subsamples, and F tests for differences among herbicide application rates thus utilized the mean squares for the treatment-by-replication interaction as an error term. Root damage (scored) data were subjected to square root transformations, $(\text{rating or count} + 1)^{1/2}$, to reduce the coefficients of variation, but original ratings or count measurements were reported graphically. Contrasts of root damage ratings were grouped based on differences in means of monocot weed weights obtained due to variable herbicide application rates. Contrasts were designed to evaluate weed interference as created by predetermined levels of a standard herbicide rate. Weed populations could only be determined after herbicide application. Contrasts of protein, thousand kernel weight, and oil analysis were based on 0 vs. 100% of herbicide application rates. These contrasts were designed to compare herbicide vs. no herbicide effects on crop quality.

A3.3 Results and Discussion

A3.3.1 Weed Biomass and Dockage in Response to Herbicide Rate

Monocot weed dry weights were significantly affected by herbicide application rates (Table A3.1). Herbicide rate was responsible for most of the variation in weed biomass as shown by the coefficient of determination (R-square) values reported in Table A3.1. Coefficients of determination, based on log-transformed data, ranged from 97% in 2004 Lacombe *B. rapa* plots to 65% in 2005 in *B. napus* plots in Lacombe. In all locations and years the R-square values were higher in *B. rapa* than in *B. napus* plots (Table A3.1). For instances where coefficient of determination values were greater than 90%, the regression curves indicated linear or curvilinear responses in reductions in monocot weed dry weights with increases in herbicide application rates (Figure A3.1).

Weed populations were extremely variable in different sites and years. For example, the monocot weed dry weights in untreated plots of *B. rapa* at Lacombe in 2004 were only 1.0% of those observed in 2003 (9.95 in 2004 vs. 976.63 kg ha^{-1} in 2003), illustrating substantial weed variability during the three years of our study. Similar extremes occurred in Beaverlodge with maximum monocot dry weights in untreated plots of *B. napus* ranging from 126.3 kg ha^{-1} to 920.4 kg ha^{-1} in 2003 and 2005 respectively. This range represents a seven-fold variation in weed biomass. This variability is also evident in the log-transformed histograms presented in Figure A3.1.

Dockage values were associated with herbicide application rates. Highest dockage percentages consistently occurred in the untreated plots and lowest dockage levels were in plots treated at 80 or 100% of the registered herbicide rate. In only one instance was percent dockage not significantly associated with herbicide rate (at Lacombe in 2005 in the *B. rapa* plots) (Table A3.1). That location and year also had the

lowest R-square of all environments, with a value of only 29.3%, and may not be representative of the normal interaction between the two variables (Table A3.1). Herbicide rate was responsible for most of the variation in dockage as shown by the coefficients of determination (R-square) (Table A3.1). When coefficient of determination values were greater than 90%, the regression curves indicated linear or curvilinear responses in reductions in dockage with increases in herbicide application rates (Figure A3.2).

Monocot weed populations, as represented by their dry weights, were influenced by variable herbicide application rates at both study sites; however, in years when substantial weed populations developed in the untreated control plots, reductions in monocot weed biomass were not always proportional to the herbicide rate applied. For example, at Beaverlodge in 2003 we found no significant differences in weed biomass levels among plots treated with herbicide at rates ranging from 20 to 100% of the label rate.

A3.3.2 Seed Yield and Quality Responses to Herbicide Rate

Yields of *B. napus* significantly exceeded those of *B. rapa* in all years and locations (Figure A3.3). When compared over all years and sites (excluding Lacombe 2004 due to experimental design) for treatments that were common each year (0, 20, 40, and 100% of herbicide label application rates), only the differences between the 0% herbicide rate and the 40 and 100% rates in *B. napus* were significantly different ($P = 0.0091$ and $P = 0.0024$, respectively).

Seed oil content differed in most locations and years between canola species, with oil content of *B. napus* significantly greater than that of *B. rapa*. No significant differences were observed due to herbicide treatment in any year of the study with the exception of Beaverlodge in 2005 where herbicide application to canola at 5% of the label rate resulted in lowest seed oil content for both species ($P < 0.006$). No significant differences were observed when herbicide application rates that were common every year were compared over all seasons (2003 to 2005) and sites (excluding Lacombe 2004 due to experimental design). The R-square values for seed oil content and herbicide rate manipulation were quite low (Table A3.1), indicating a weak relationship between the two variables.

Protein content of *B. rapa* seed significantly exceeded that of *B. napus* in most locations and years ($P < 0.001$). When compared over all seasons and sites (excluding Lacombe 2004 due to experimental design) for treatments that were common over all years, no significant differences in protein content were found. The R-square values for seed protein content and herbicide rate manipulation were low (Table A3.1), indicating little association between the two variables.

Thousand kernel weights were consistently higher in the *B. napus* plots (mean range = 3.94 to 4.17 g) than in *B. rapa* plots (mean range = 2.71 to 2.82 g). At Lacombe, thousand kernel weights for each canola species were relatively similar for the different years of study. At Beaverlodge, however, thousand kernel weights were approximately 1.3-fold greater in 2004 and 2005 than in 2003 for *B. rapa*, and approximately 1.2-fold greater in 2005 than in 2003 and 2004 for *B. napus*. Herbicide application rate had no significant effect on thousand kernel weight when compared over all seasons and sites for

treatments that were common (excluding Lacombe 2004). Contrasts performed on the 0 vs. 100% herbicide rates did indicate significant differences in *B. rapa* at Beaverlodge in 2003 and 2005. Canola subjected to the 100% herbicide rate had significantly larger thousand kernel weights than canola at the 0% herbicide rate ($P = 0.0291$). However, the reverse was true in 2005 with canola at the 0% herbicide rate having significantly larger seed size than at the 100% rate ($P = 0.0339$). In both 2003 and 2005 at Beaverlodge, the coefficients of determination were highest compared with other years and responses (Table A3.1). In both situations where contrasts were significant, the regression responses were linear.

I found no significant differences in crop quality characteristics (seed oil and protein contents, thousand kernel weights) that were attributable to herbicide applications at different rates (Table A3.1). This could indicate that no such relationship between crop quality and herbicide rate exists, or that the experimental design did not enable detection of these changes. Thousand kernel weights were quite variable by year and site. Although no significant differences were found in the ANOVA, significant differences were found with contrasts between 0 and 100% herbicide rates at Beaverlodge for *B. rapa* in 2003 ($P = 0.0291$) and 2005 ($P = 0.0339$). However, opposite effects were observed: in 2003, higher thousand kernel weights occurred in plots subjected to the full (100%) label application rate, while in 2005 higher kernel weights occurred at the 0% rate. The reasons for this discrepancy are unclear. Weed biomass levels were adjusted for monocot weed species only, and it is possible that application of the dicot herbicides interfered with anticipated changes in crop quality at low application rates of the monocot herbicide used. However, those differences were only observed

when the R-square values were highest (Table A3.1). Further research is needed to address this issue, perhaps using an experimental design restricted to the use of monocot herbicide only.

High weed densities did not always correspond with yield losses: for instance at Lacombe in 2003 weed populations were very high in plots subjected to the 0 and 20% herbicide rate treatments, yet this did not translate into significant yield losses. Herbicide rates were adjusted in 2004 and 2005 in an attempt to obtain a more gradual decline in weed populations with increasing herbicide rate. This approach was successful, but yield was not always affected significantly. Over all years and sites, only the yields for *B. napus* in the 0 vs. 40% and 0 vs. 100% contrasts were significant statistically. Based on the three regression equations of O'Donovan et al. (2005) for wild oats and volunteer cereals in canola, predicted yield losses were 20 to 35%. Evidently other environmental, genetic, and biotic factors may influence weed populations and the yield reductions they cause. For instance, other weed management practices, besides herbicide application rate, can affect crop losses due to weeds and the resulting economic risk involved (Kirkland et al., 2000; O'Donovan et al., 2003a, 2003b), and yield losses due to weeds can be influenced by crop genotype, weed phenology, and soil moisture and fertility levels (Liebman et al., 2001).

A3.3.3 Interactions Between Root Maggot Infestations and Herbicide Rate

Egg deposition counts were extremely low throughout the 2003 and 2004 seasons, resulting from dry soil conditions. This trend continued into 2005, due to low root maggot adult populations. Egg deposition did not vary between canola species ($P >$

0.05), and on average a mean of only approximately one egg per plant was recorded. When data were analyzed over all seasons (2003 to 2005) and sites (excluding Lacombe 2004), no significant effects of treatment with different herbicide application rates were observed ($P > 0.05$).

In most years, mean root maggot damage ratings in plants of *B. rapa* significantly exceeded those of *B. napus* ($P < 0.05$) (Figure A3.3). Mean root maggot damage rating and herbicide rate were not usually correlated. However, at Lacombe in 2004, contrasts of high versus low herbicide rates, with the contrast groupings based on monocot weed dry weights achieved through herbicide variations, resulted in a significant difference for *B. napus* ($P = 0.0297$) (Figure A3.4a). Here, monocot weed dry weight declined with an increase in herbicide application rate, and this was accompanied by corresponding increases in mean root maggot damage ratings, especially for rates ranging from 10 to 100% of the label rate. Similar contrasts for *B. rapa* were not significant ($P = 0.4692$). At Lacombe in 2005, differences between herbicide application rates were also significant, with the 40% rate highest in mean damage ratings for both canola species. When grouped with respect to monocot weed biomass, the 40 and 100% herbicide application rates were associated with lowest weed biomass levels, but highest mean root maggot damage ratings that were significantly greater than for lower application rates in *B. rapa* ($P = 0.0372$) (Figure A3.4b), but not in *B. napus* ($P = 0.4384$).

In canola agroecosystems, early weed removal is often recommended for optimal yields in western Canada (Clayton et al., 2002; Martin et al., 2001; O'Donovan, 1992), but this practice can be associated with increased root maggot damage. Dosdall et al. (2003) found that root maggot damage and oviposition declined with a delay in weed

removal from the two- to the six-leaf stages of canola development. Among several ecological hypotheses given in the literature to explain lower insect populations and their associated damage in heterogenous cropping systems (Altieri and Letourneau, 1984), it was proposed that weeds interfered with the behavioural sequence of events required by *D. radicum* females prior to oviposition, leading to reduced infestation levels in these systems (Dosdall et al., 2003). In this study, only two of 12 contrasts between root maggot damage ratings grouped by monocot weed dry weights were significant (Figure A3.4). The absence of more frequent associations between root maggot infestations and monocot weed densities was likely a reflection of the substantial decline in *Delia* spp. populations that occurred between 2002 and subsequent years. Both study sites experienced severe drought in 2002, with only 151.7 and 178.2 mm of precipitation received at Lacombe and Beaverlodge, respectively, during the entire growing season (May to September) compared with long-term normal values of 342.7 and 282.7 mm (Table A3.1). Root maggot population densities are positively correlated with soil moisture content (Griffiths, 1986b). Drastic reductions in populations of the two most abundant root maggot species, *D. radicum* and *D. platura*, were subsequently observed at the study sites (Broatch et al., 2006), and these were likely attributable to failure of root maggot populations to fully recover from the 2002 drought. Nevertheless, the significant interactions that did occur as documented here and in Dosdall et al. (2003) indicate that an interaction exists between root maggot infestations and weeds; however, the natural variability in environmental conditions makes it difficult to exploit this relationship for improved integrated crop management.

Weedy backgrounds can influence humidity and solar radiation levels in the crop canopy, as well as other aspects of the microclimate like availability of protective refugia (Landis et al., 2005; Pavuk et al., 1997), and these in turn could influence the abundance of root maggot predator-parasitoids like *Aleochara* spp. (Coleoptera: Staphylinidae), or perhaps carabid beetle species that also feed on weed seeds. For instance, Kromp (1989) found that carabid beetle numbers were higher in biologically managed fields due to their greater weediness and heterogeneity, and the absence of pesticides. Several studies have associated higher ground beetle numbers with weedy situations (Norris and Kogan, 2000), but the effects of weedy backgrounds on natural enemies of insect pests and on insects that consume weed seeds are important relationships that remain to be investigated in canola cropping systems.

Root maggot damage levels varied considerably between sites, and in general, mean damage at Beaverlodge exceeded that observed at Lacombe, especially in 2003 and 2004. Environmental characteristics of the two sites can explain these differences in root maggot infestation levels. Beaverlodge is situated approximately three degrees latitude further north than Lacombe, and so receives longer periods of sunlight during the growing season. Soil type is also quite different: the luvisolic clay loam soil of Beaverlodge has higher clay content than the chernozemic loam of Lacombe. The different soil types support microbial populations that vary substantially between sites. Brown girdling root rot (*Rhizoctonia solani* Kühn) occurs only occasionally in the ecoregion that encompasses Lacombe, but in northern Alberta it is widespread and causes substantial yield losses (Thomas, 2002; Klein-Gebbinck and Woods, 2002). Root maggot damage to canola is often exacerbated by secondary invasions of pathogenic fungi

(Griffiths, 1986a); therefore, similar levels of initial attack and feeding by *Delia* spp. larvae may be compounded by invading fungi and bacteria. Higher mean root damage levels to canola at Beaverlodge could then be a reflection of environmental conditions that foster greater secondary attack by phytopathogens.

Although the relationship between root maggot infestation levels and monocot weed densities was not evident in all sites and years of our study, its occurrence at Lacombe in 2003 and 2005 emphasizes the importance of adopting management practices that are compatible for both weed and root maggot control, as proposed by Dosdall et al. (2003). In a comprehensive review of integrated weed management approaches for spring-sown crops in western Canada, O'Donovan et al. (2007) proposed integrating reduced herbicide rates with agronomic practices that improve crop competitiveness over weeds because herbicides can sometimes perform more efficaciously in the presence of crop competition. Reducing herbicide application rate may then be another compatible management strategy for both pests that has been inadequately exploited in canola cropping systems, especially when used in combination with competitive varieties.

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Table A3.1: Coefficient of Determination (R-Square) and Coefficient of Variation (CV) values obtained through regression analysis for monocot weed dry weights (kg ha^{-1}), percent seed protein and oil contents, thousand kernel weights, and percent dockage or contamination of crop seed with weed seed and other material for canola treated with the herbicide sethoxydim at the recommended application rate (100%) or various reduced rate applications for the Lacombe and Beaverlodge, AB study sites in 2003 to 2005, on *Brassica rapa* and *Brassica napus* plots.

Site/year	Species	Monocot weed * dry weight (kg ha^{-1})		Canola agronomic quality parameters: % Protein		% Oil		Thousand kernel weight (g)		% Dockage *	
		R-square	CV	R-square	CV	R-square	CV	R-square	CV	R-square	CV
Beaverlodge											
2003	B. rapa	83.6	13.251	8.0	5.443	8.5	2.103	42.7	5.734	43.6	11.697
	B. napus	73.4	17.028	5.9	5.595	12.2	1.839	36.8	4.360	68.7	8.997
2004	B. rapa	95.3	6.465	11.7	2.098	9.1	1.840	8.2	12.188	95.3	6.465
	B. napus	94.3	8.133	17.6	3.155	15.0	2.396	17.9	10.056	91.5	4.116
2005	B. rapa	85.2	6.158	28.4	2.727	14.2	1.267	38.9	10.417	95.4	3.523
	B. napus	84.7	7.419	16.6	3.482	23.4	1.651	33.3	3.892	97.4	3.800
Lacombe											
2003	B. rapa	86.8	28.161	9.1	5.893	6.2	2.262	1.0	4.081	83.9	12.739
	B. napus	78.8	29.589	11.0	6.765	9.5	2.250	20.8	5.315	91.3	6.329
2004	B. rapa	97.0	9.790	1.3	2.408	3.9	0.821	7.3	8.978	98.0	4.094
	B. napus	95.1	13.558	16.5	4.177	26.0	1.285	18.9	3.156	93.6	8.385
2005	B. rapa	77.6	7.899	19.2	3.376	17.1	1.948	15.7	3.577	29.3	11.227
	B. napus	65.0	12.610	8.4	5.686	9.3	2.275	12.3	7.812	64.9	13.469

* Log transformations were required to reduce the coefficients of variation for weed dry weight and dockage values.

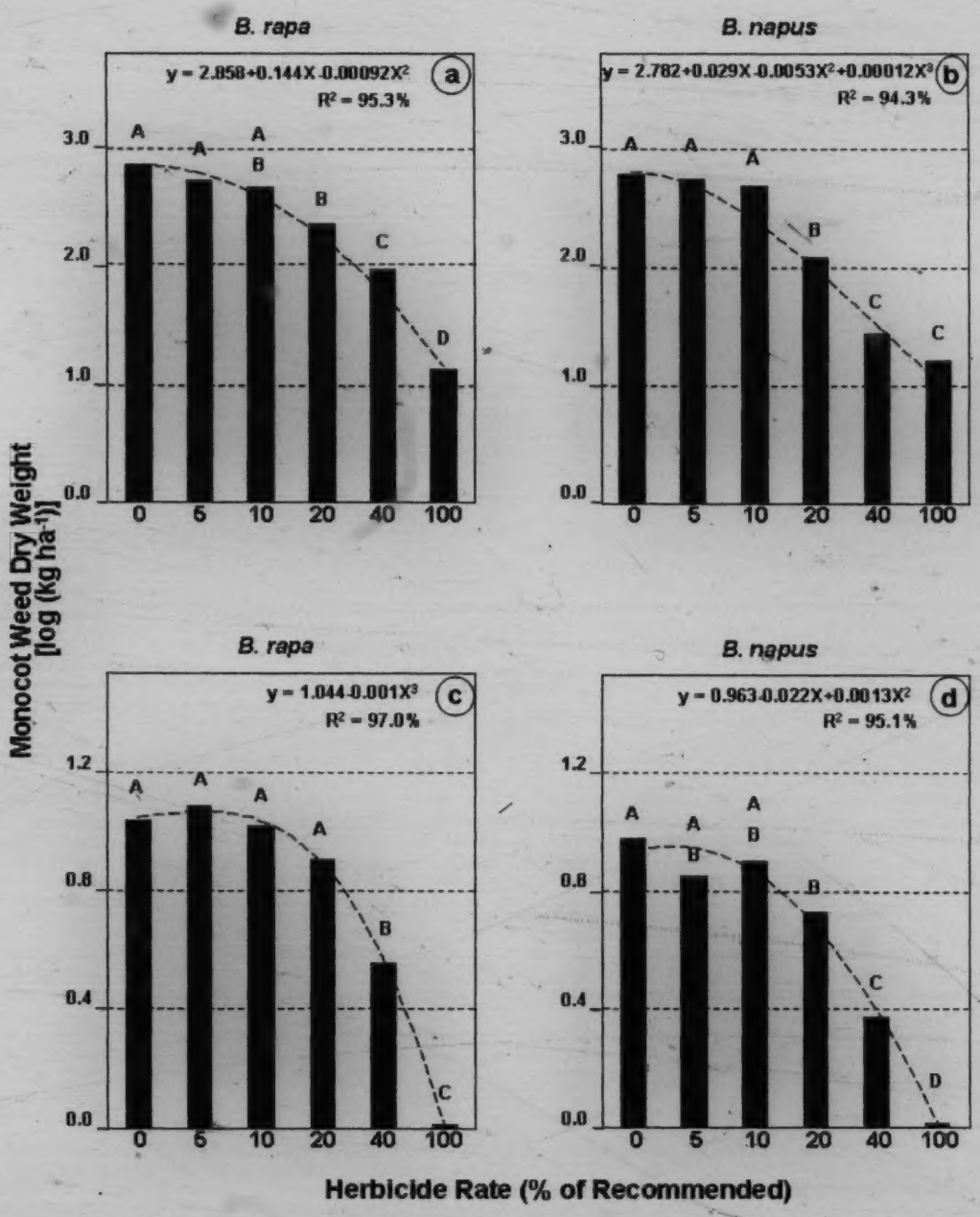

Figure A3.1: Mean monocot weed dry weights [log (kg ha^{-1})] for canola treated with the herbicide sethoxydim at various application rates for: (a) Beaverlodge, AB in 2004 on *Brassica rapa* plots; (b) Beaverlodge, AB in 2004 on *Brassica napus* plots; (c) Lacombe, AB in 2004 on *B. rapa* plots; and (d) Lacombe, AB in 2004 on *B. napus* plots. Letters on histograms indicate Tukey's Studentized Range Test groupings, and the solid line presents the regression line for the relationship.

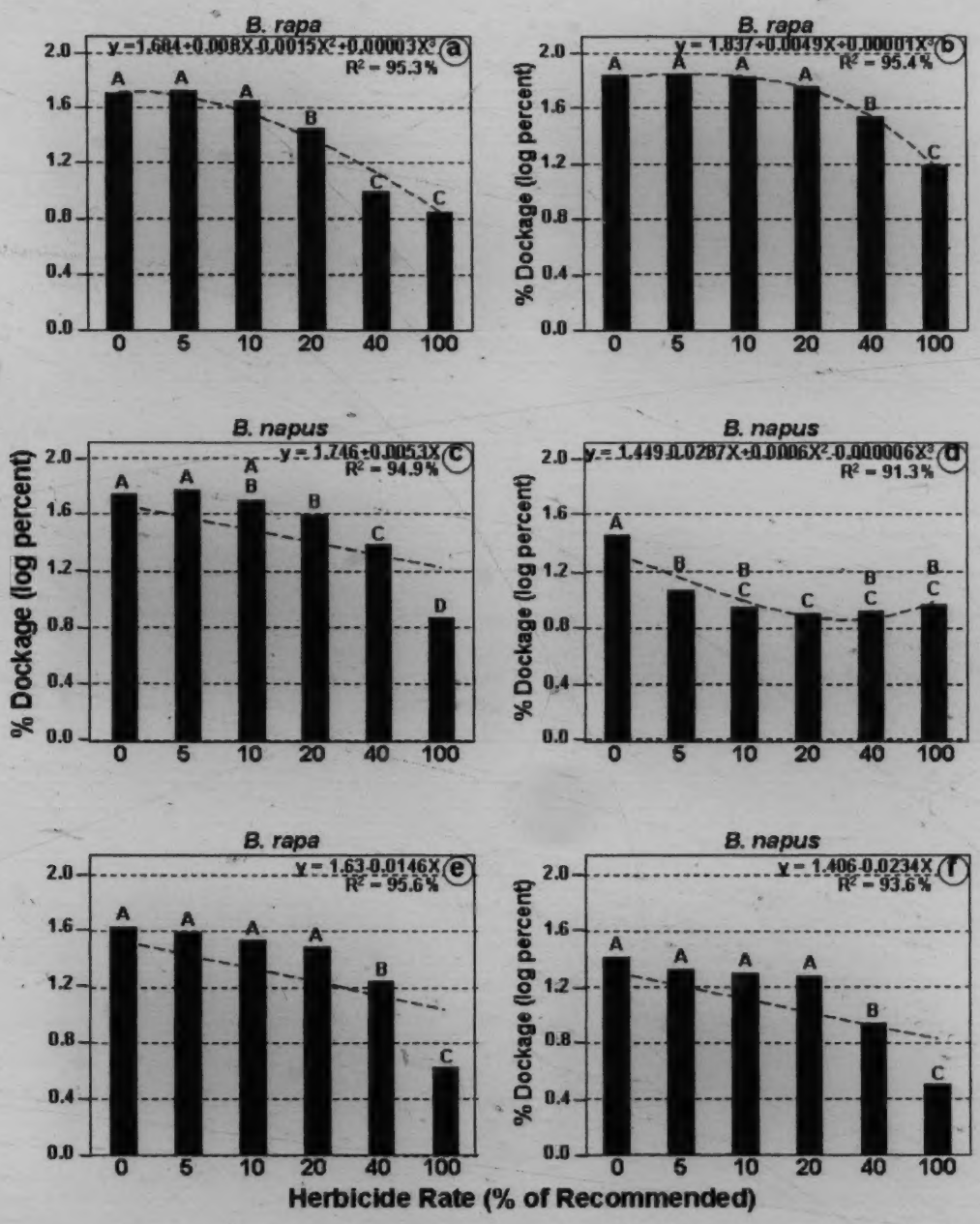

Figure A3.2: Mean percent dockage (log transformed) for canola treated with the herbicide sethoxydim at various application rates for: (a) Beaverlodge, AB in 2004 on *Brassica rapa* plots; (b) Beaverlodge, AB in 2005 on *Brassica rapa* plots; (c) Beaverlodge, AB in 2005 on *B. napus* plots; (d) Lacombe, AB in 2003 on *B. napus* plots; (e) Lacombe, AB in 2004 on *B. rapa* plots; and (f) Lacombe, AB in 2004 on *B. napus* plots. Letters on histograms indicate Tukey's Studentized Range Test groupings, and the solid line presents the regression line for the relationship.

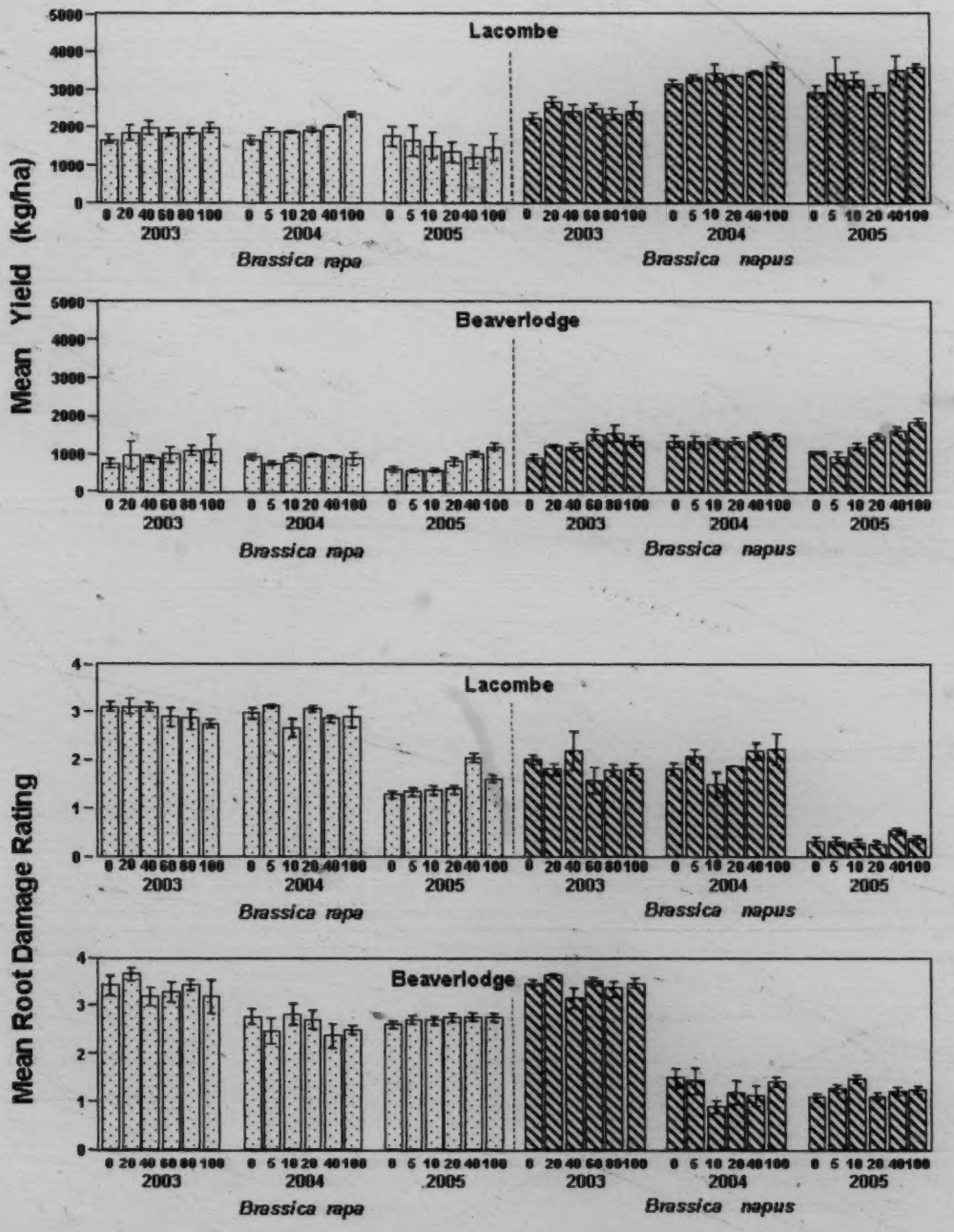

Figure A3.3: Mean yields and root maggot damage ratings per plot (± S.E.) of *Brassica rapa* (cv. Hysyn 110) and *Brassica napus* (cv. InVigor 2733) subjected to different application rates of sethoxydim herbicide (0 to 100%) to control monocot weed populations at Beaverlodge and Lacombe, AB during 2003, 2004, and 2005.

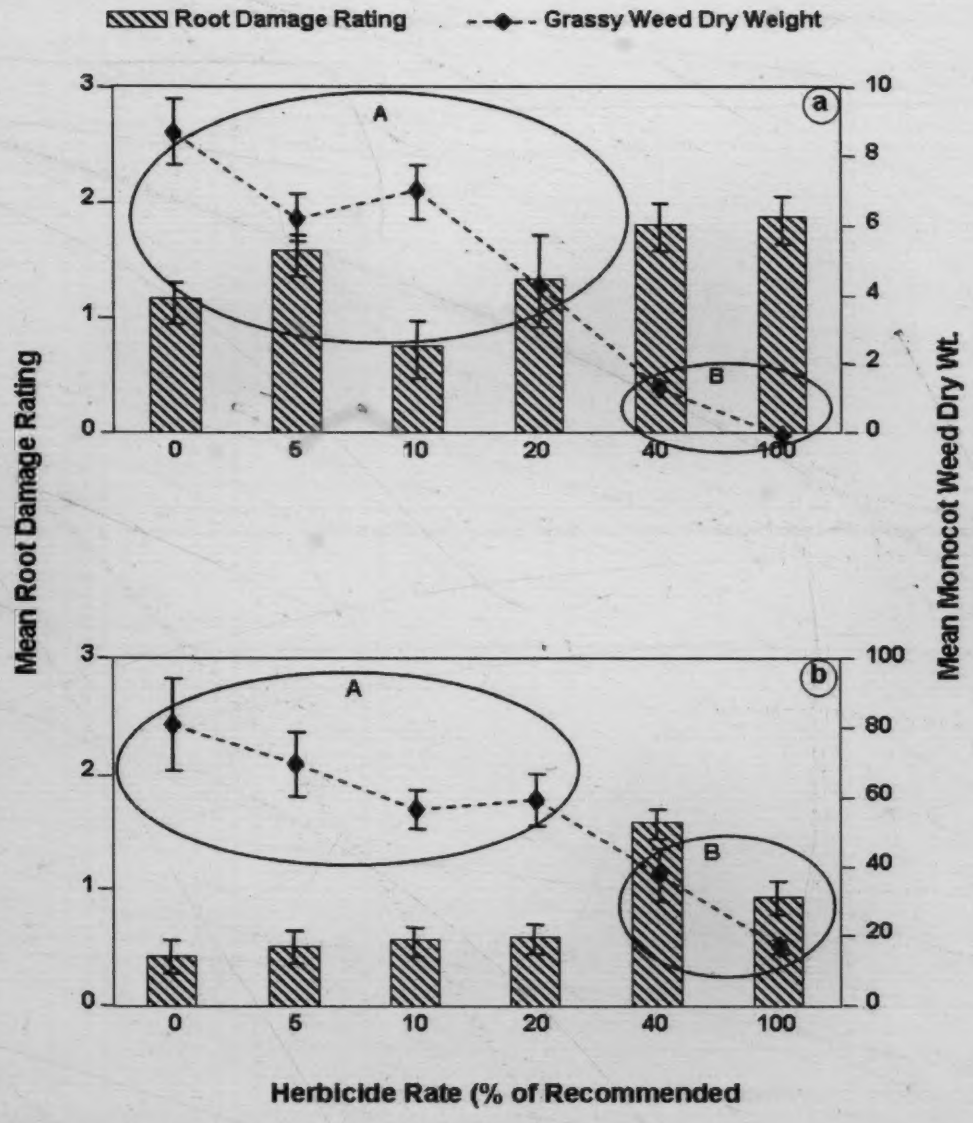

Figure A3.4: Contrasts between mean root maggot damage ratings (± S.E.) and mean monocot weed dry weights (± S.E.) of Group A, comprising sethoxydim herbicide applied at 0, 5, 10, and 20% of the registered label rate, and (a) Group B, comprising herbicide applied at 40 and 100% of the label rate for *Brassica napus* cv. InVigor 2733 at Lacombe, AB in 2004 ($P = 0.0297$); and (b) Group B, comprising herbicide applied at 40 and 100% of the label rate for *B. rapa* cv. Hysyn 110 at Lacombe, AB in 2005 ($P = 0.0372$).

Chapter 4: Emergence and Seasonal Activity Patterns of the Entomophagous Rove Beetle *Aleochara bilineata* (Coleoptera: Staphylinidae) in Canola in Western Canada[1]

[1] *Note*: A version of this chapter has been accepted for publication:

Broatch, J.S., L.M. Dosdall, R.-C. Yang, K.N. Harker, and G.W. Clayton. Emergence and seasonal activity patterns of the entomophagous rove beetle *Aleochara bilineata* (Coleoptera: Staphylinidae) in canola in western Canada. *Environmental Entomology*, in press.

4.1 Abstract

Aleochara bilineata Gyllenhal (Coleoptera: Staphylinidae) is an important natural enemy of root maggots (*Delia* spp.) (Diptera: Anthomyiidae), which are serious pests of brassicaceous crops in North America and Europe. Adults of *A. bilineata* feed on eggs and larvae of root maggots, and *A. bilineata* larvae parasitize *Delia* spp. pupae. Emergence and seasonal activity patterns of *A. bilineata* were investigated during 2003 to 2005 in canola (*Brassica rapa* L. and *Brassica napus* L.) in central Alberta, Canada in relation to degree-day accumulations and Julian date. Pitfall trap captures of *A. bilineata* adults within emergence cages situated over canola stubble from the previous year indicated that approximately 428, 493, and 455 degree-days (soil base 5.57°C) and 187, 189, and 180 Julian days were required for 50% emergence in 2003, 2004, and 2005 respectively (three-year mean = 185.1 ± 2.8 Julian days (SEM)). Pitfall traps placed in current canola crops determined that 50% levels of activity density required 534, 380, and 559 degree-days and 195, 180, and 186 Julian days respectively in each of the three years. A logistic model that described the relationship of degree-days and Julian days

with emergence of adult beetles was appraised, and good correspondence was evident between predicted and observed cumulative emergence patterns. Emergence and seasonal activity periods of *A. bilineata* in canola were well synchronized with occurrence of pre-imaginal life stages of its principal hosts, *Delia radicum* (L.) and *Delia platura* Meigen, with beetle emergence beginning shortly after the onset of root maggot oviposition.

4.2 Introduction

Aleochara bilineata Gyllenhal (Coleoptera: Staphylinidae) is a predator and parasitoid of cyclorrhaphous Diptera, including several important pest species of brassicaceous crops like the cabbage maggot, *Delia radicum* (L.), the seedcorn maggot, *Delia platura* (Meigen), the turnip maggot, *Delia floralis* (Fallén), and *Delia planipalpis* (Stein) (Read, 1962; Klimaszewski, 1984; Maus et al., 1998). *Aleochara bilineata* is probably native to Europe, but was accidentally introduced to North America and is now widely distributed throughout the Nearctic region (Klimaszewski, 1984).

In crops of canola, *Brassica napus* L. and *Brassica rapa* L. (Brassicaceae), the life history of *A. bilineata* is linked with that of its primary host, *D. radicum*. In June, females of *D. radicum* oviposit on or near canola plants in the rosette stage (Dosdall et al., 1994), and larvae tunnel through taproots feeding primarily on periderm and vascular tissues (McDonald and Sears, 1992). Feeding by root maggot larvae can disrupt the flow of water and nutrients within canola plants, and provides an invasion pathway for root rot fungi, which together can cause crop losses of many millions of dollars (Can.) annually

(Griffiths, 1986; Soroka et al., 2004). Late in the season, final-instar larvae pupariate in surrounding soil or sometimes within larval feeding channels (Griffiths, 1986).

Adults of *A. bilineata* are voracious predators of *D. radicum* eggs and larvae, with a single adult beetle capable of consuming an average of 23.8 eggs or 2.6 larvae per day (Read, 1962). Read (1962) concluded that under optimum conditions a single pair of *A. bilineata* adults could destroy approximately 1,210 eggs and 128 larvae in their lifetimes. Each *A. bilineata* female can produce approximately 9 to 15 eggs per day or 700 eggs in its lifetime (Colhoun, 1953; Fournet et al., 2000). Larvae of *A. bilineata* hatch in 3 to 7 d, and first instars locate root maggot puparia. After chewing an opening in the puparial wall over a period of 12 to 36 h, the larva eventually consumes the developing pupa within (Royer et al., 1998). Overwintering of *A. bilineata* occurs as a first instar within the puparium, and new generation adults emerge the following spring (Colhoun, 1953). Acting as both a predator and a parasitoid, *A. bilineata* is an important biological control agent of cabbage maggot populations (Mukerji, 1971). In western Canada, parasitism of cabbage maggot puparia by *A. bilineata* in cole crops can be as high as 94% (Turnock et al., 1995).

The effectiveness of *A. bilineata* as a biological control agent for root maggots in canola in western Canada may be limited if its life cycle does not coincide well with vulnerable life stages of its hosts. For example, Read (1962) found that in Prince Edward Island, Canada, *A. bilineata* emerges too late to be effective for controlling first generation *D. radicum*. By contrast, in France Fournet et al. (2000) considered *A. bilineata* to be a promising biocontrol agent against *D. radicum* because its development was well synchronized with that of its host even though the beetle was found 11.5 d later

than its host in the field. Little is known of the population dynamics of *A. bilineata* in relation to its root maggot hosts in canola cropping systems in western Canada. Degree-day and logistic models were developed recently for *D. radicum* and *D. platura*, the key hosts of *A. bilineata* in canola (Jyoti et al., 2003; Broatch et al., 2006). Development of similar models for the predator-parasitoid can facilitate improved understanding of the life cycle synchrony between the herbivore and its principal natural enemy, and can serve to drive research toward identifying appropriate agronomic or biocontrol strategies for enhancing parasitoid effectiveness. In this study I determined emergence and seasonal activity patterns for *A. bilineata* in canola in western Canada, and I appraised degree-day and Julian day logistic models for predicting emergence and activity patterns of *A. bilineata*.

4.3 Materials and Methods

4.3.1 The Study Site

Experiments were conducted during 2003, 2004, and 2005 at the Agriculture and Agri-Food Canada Research Station, Lacombe, AB (113°44′W; 52°28′N). Soils at the site developed on glacial lacustrine deposited material (Bowser and Peters, 1951). Plots seeded to *B. napus* and *B. rapa* were on black Chernozemic clay loam soil (43% sand, 21% silt, and 36% clay) with a pH of 5.9 and 8.2% organic matter content.

4.3.2 Weather Data Collections and Degree-day Determinations

Degree-day accumulations were derived from soil temperatures measured at a depth of 5 cm, the depth commonly inhabited by root maggot puparia. Beginning 1 April

of each year, the minimum and maximum temperature were recorded every 5 min and measured with a Type E thermocouple on a Campbell Scientific CR10 data-logger (Campbell Scientific Canada, Edmonton, AB, Canada). The maximum and minimum temperatures from each day were used to produce the daily means.

Degree-day calculations were computed using the equation of Arnold (1960). From studies conducted in Europe, Langlet (1997) reported that the base temperature for development of *A. bilineata* was 5.57°C. This developmental threshold was subsequently confirmed by Brunel et al. (1999) and adopted in this study.

4.3.3 Insect Sampling and Canola Development

Each year, emergence and activity dynamics of field populations of *A. bilineata* were investigated using two regimes of pitfall trapping. In the first trapping regime, pitfall traps were deployed in *B. rapa* and *B. napus* seeded in spring of the same year when the samples were collected ("current crop sampling"). In the second regime, pitfall traps were placed within emergence cages established over canola stubble ("emergence sampling"), in an area seeded to canola in the preceding year.

For current crop sampling, *B. napus* cv. InVigor 2733 and *B. rapa* cv. Hysyn 110 were seeded at Lacombe on 2 May 2003, 17 May 2004, and 10 May 2005. The area seeded to each canola species encompassed 2,880 m^2 and was fertilized at 100% of the soil test recommendations for canola production. Canola was seeded into cereal stubble with a ConservaPak® drill with 30.5 cm row spacings at a density of 150 seeds m^{-2}. In 2003, 48 pitfall traps were deployed: 24 in the area seeded to *B. napus* and 24 in *B. rapa*. In 2004 and 2005, 48 traps were placed in each crop species. Pitfall traps were

distributed uniformly along a transect throughout the site, but were at least 3 m in from the edges of the canola and separated from each other by distances of approximately 15 (2003) and 8 m (2004, 2005). Developmental stages of plants of *B. napus* and *B. rapa* were recorded weekly using the scale recommended by Thomas (2002).

During emergence sampling, cages were set out in early April of each year, on canola plots harvested in the preceding autumn. The cages followed the design of Dosdall et al. (1996a), measured 1 by 1 m at the base, and were covered in fine mesh screening to prevent escape of insects that emerged within the cages. In the preceding year, *B. napus* (InVigor 2733) and *B. rapa* (Hysyn 110) were each grown on the site over an area of approximately 720 m^2 after being seeded into cereal stubble with a ConservaPak® drill with 30.5 cm row spacing at a density of 150 seeds m^{-2}. In 2003, 32 emergence cages were used, with 16 each in *B. rapa* and *B. napus* stubble. In 2004 and 2005, 48 emergence cages were used, with 24 each in *B. rapa* and *B. napus* stubble.

In both sampling regimes, pitfall traps consisted of two GenPak® plastic cups placed one inside the other. Cups had a diameter of 11 cm, a depth of 15 cm, and were filled to a depth of 5 cm with propylene glycol. A 17 by 17 cm rain cap was placed about 5 cm above each trap. Pitfall traps within the emergence cages did not have rain caps. An observation and maintenance port on one side of each emergence cage allowed collection, replacement, and maintenance of the pitfall trap within the cage. These openings were sealed except during sample collections.

Pitfall trap collection and replacement occurred approximately weekly. The inner sleeve components of the traps were removed from the field and taken to the laboratory for processing. Trap contents were preserved in 70% ethanol until specimens could later

be sorted, identified, and data recorded.

4.3.4 Species Identifications, Voucher Specimens, and Sex Determinations

Identifications of *A. bilineata* specimens were performed using Klimaszewski (1984) with representative species identifications verified by J. Klimaszewski. Voucher specimens from the study have been deposited in the Strickland Museum of Entomology, University of Alberta, Edmonton, AB and at the Agriculture and Agri-Food Canada Research Centre in Lacombe, AB.

Sex was determined for each specimen in the emergence study through dissection, and comparison with line drawings in Klimaszewski (1984). Sex was reported as percentages of overall emergence of males and females for that year, based on the dates when they were removed from the emergence traps. When sex determination was not possible because adults lacked complete abdominal structures (e.g., the aedeagus or spermatheca), the specimens were not included in the totals. Damage to these structures sometimes occurred from breakage during pinning or while in ethanol.

4.3.5 Model Development and Data Analysis

A logistic model was appraised that described the relationship of degree-days or Julian days with the emergence patterns of adult beetles for each year and the combination of years. This model was then used to predict the total degree-days and Julian days required for emergence of 10, 25, 50, 75, and 95% of the beetle population. We used the following equation for the logistic model (Davidson, 1944):

$$Y = a + \frac{c}{1 + \exp\{-b(x - m)\}} \qquad [4.1]$$

where Y is the percent emergence, x is either the summation of Julian days or degree-days, a is the lower asymptote, c is the upper asymptote, m is the Julian day or degree-day requirements for maximum emergence (or inflection point), and b is the slope.

Where the relationship between degree-days and Julian days fit a linear regression model we used the following equation:

$$Y = a + b\,x \qquad [4.2]$$

where Y is the percent emergence, x is either the summation of Julian days or degree-days, a is the Y intercept, and b is the slope.

Means and standard errors used in graphs and tables describing the adult captures from all traps per week for each year were calculated using PROC MEANS (SAS Institute Inc., 2004). Estimates of the four parameters (a, b, c, and m) as given in the logistic and linear models were obtained through PROC MODEL (SAS Institute Inc., 2004). Logistic calculations of the percent emergence of populations were calculated with Microsoft Excel® computer software. Homogeneity of responses across three years was determined from the significance of the tests for interactions, Year by Degree-days and Year by Degree-days by Degree-days, as implemented in SAS PROC MIXED (SAS Institute Inc., 2004).

4.4 Results

4.4.1 Environmental Conditions and Plant Development

Precipitation at Lacombe during the 2003 growing season exceeded long-term normal values (1908-2005) during April and May by about 40 mm, but was below average levels from June to August by approximately 118 mm. However, precipitation

patterns during 2004 and 2005 were much closer to long-term mean values. Residual soil moisture levels from snow melt were sufficient to ensure uniform germination and emergence of canola seedlings.

Mean air temperatures during 2003 to 2005 approximated long-term average values, although temperatures during August 2003 were warmer than average (Table 4.1). Mean monthly soil temperatures were usually warmest during 2004 (Table 4.1). Seasonal degree-day totals accumulated during the growing season (base 5.57°C) were similar for the years 2003 to 2005 with 1103.8, 1129.6, and 1118.7 degree-days accumulated, respectively.

In 2003, flowering (Stage 61 of Thomas, 2002) of *B. rapa* and *B. napus* began on 27 June and 2 July, respectively, and ended (Stage 69 of Thomas, 2002) on 13 and 16 July. In 2004, flowering began on 28 June and 5 July and ended on 16 and 20 July. In 2004, the onset of flowering occurred on 30 June and 6 July for *B. rapa* and *B. napus*, respectively, and ended on 13 and 20 July.

4.4.2 Emergence Trap Captures of *A. bilineata*

In total, 250, 131, and 88 adults of *A. bilineata* were captured in pitfall traps within the emergence cages during 2003 to 2005, respectively. Trap captures were highest in 2003 compared with 2004 and 2005, with approximately three times more adults collected in 2003 than in 2005. There were significant ($P < 0.05$) interactions for Year by Degree-days and for Year by Degree-days by Degree-days for degree-days but not for Julian days, indicating that responses to Julian days were homogeneous, but responses for degree-days were heterogeneous.

In 2003 and 2004, the first captures of *A. bilineata* adults occurred on approximately 20 June in the emergence traps, but in 2005 adults were first collected a few weeks sooner (Figure 4.1). Peak captures of *A. bilineata* occurred during 5 to 11 July 2003 (sampling period 27), which corresponded to approximately 478 degree-days and Julian days 186 to 192. Two weeks later trap captures declined to near zero and remained at this level for the remainder of the season. Trap captures peaked during 10 to 16 July 2004 (sampling period 28) or during Julian days 191 to 198 after approximately 580 degree-days, and during 1 to 7 July 2005 (sampling period 27) or during Julian days 181 to 188 after approximately 550 degree-days.

Estimated requirements for emergence of 50 and 75% of the *A. bilineata* population were 428 and 476, 493 and 572, and 455 and 532 degree-days for 2003, 2004, and 2005, respectively (Table 4.2). The mean requirements for emergence of 50% of the population, as determined by logistic analysis, corresponded to the Julian date of 185.12 ± 2.81 or about 4 July in most years, which is slightly earlier than the observed peak capture periods (Figure 4.1). This date corresponds to canola flowering (Stage 61 of Thomas, 2002). All emergence trap captures could be described using logistic analysis (Table 4.3). Analysis of 2004 data could not predict the upper end of the logistic curve. Mean Julian day requirements (± S.E.) based on homogeneous responses over the three years of study for emergence trap collections for 10, 25, 50, 75 and 95% emergence were 171.82 ± 3.80, 178.51 ± 3.20, 185.12 ± 2.81, 191.48 ± 2.63, and 200.77 ± 1.88. Comparisons of predicted and observed cumulative emergence patterns for 2003 and 2005 indicated good correspondence, particularly for 2003, with sigmoid patterns evident in both years (Figure 4.2).

Percent emergence of male and female *A. bilineata* was approximately equal over each trapping period during 2003 to 2005, but more than twice as many males as females emerged in 2004 (Figure 4.3). In 2003, of 226 adults dissected, 112 were males and 114 were females. In 2005, of 84 adults dissected, 41 were males and 43 were females. In 2004, however, 90 males and 37 females were recorded of 127 adults dissected.

4.4.3 Captures of *A. bilineata* in Current Canola Plots

A total of 524 adult *A. bilineata* were collected in pitfall traps in canola plots during 2003. No major peaks in beetle activity were observed (Figure 4.4). Logistic analysis could not be performed because the population followed a linear response (Table 4.3). Flowering in canola, which began on 27 June (*B. rapa*) and 2 July (*B. napus*), was not associated with major peaks in *A. bilineata* captures. Results of the linear analysis for degree-day and Julian day requirements for 10, 25, 50, 75, and 95% emergence of *A. bilineata* adults from collections in open pitfall traps estimated that substantially more degree-days and Julian days were required for 50 and 75% emergence of *A. bilineata* than for emergence trap collections estimated with logistic analysis; however, fewer degree-days and Julian days were needed for 10 and 25% emergence with linear analysis (Table 4.2). In the combined analysis there were significant Year by Degree-day and Year by Degree-day by Degree-day interactions for degree-days and Julian date. Therefore responses to Julian date and degree-days were heterogeneous and not included in any mean calculation.

A total of 2,965 adult *A. bilineata* were captured in pitfall traps in the current canola crop during 2004. Trap captures were low early in the season until 10 June but

thereafter numbers increased rapidly to a maximum from 18 to 30 June (sampling periods 24 and 25), which corresponded to Julian days 170 to 182 (Figure 4.4). The population peak corresponded to plants in late rosette (Stage 33) to early flowering (Stage 61). Estimates for degree-day and Julian day requirements for 10, 25, 50, 75, and 95% emergence of *A. bilineata* adults using logistic analysis were higher using data from emergence than current crop sampling (Table 4.2). For example, with emergence trap data, 50 and 75% emergence of the *A. bilineata* population occurred after 493 and 572 degree-days or Julian days 189 and 196, but the current crop collections estimated these values at 379 and 470 degree-days or Julian days 180 and 188 (Table 4.2).

In 2005, a total of 621 adults were captured in the current canola crop. The pattern of captures did not allow for a logistic analysis, and the best representation was a linear trend (degree-day $r^2 = 92.98$, Julian date $r^2 = 94.12$). An early-season peak was evident during 4 to 10 June (sampling period 22 or Julian days 155 to 161) that correlated with canola in early rosette or early bolting (Stage 30) (Figure 4.4). May 2005 had the warmest soil and air accumulations of the three years of the study (Table 4.1), and was also the driest of the three years. Two peaks occurred later in the season, 1 to 7 July (sampling period 26 or Julian days 182 to 188) and 28 July to 4 August (sampling period 30 or Julian days 209 to 216). The early July peak coincided with the beginning of flowering (Stage 59). The early August peak coincided with the *A. bilineata* peak observed in current crop collections during 2003 (Figure 4.4). Results of the linear analysis for degree-day and Julian day requirements for 10, 25, 50, 75, and 95% emergence of *A. bilineata* adults from collections in current crop pitfall traps estimated that substantially more degree-days and Julian days were required for 50, 75, and 95%

emergence of *A. bilineata* than estimates obtained with logistic analysis for captures in emergence traps; however, fewer degree-days and Julian days were needed for 10 and 25% emergence with linear analysis (Table 4.2).

Estimates for degree-day and Julian day requirements for emergence of *A. bilineata* adults based on linear analysis were usually slightly higher for adult collections from the current crop versus emergence pitfall traps (Table 4.2). For example, estimates for 2003 and 2005 indicate that 105 and 104 more degree-days, respectively, were required for 50% emergence of *A. bilineata* in the current crop than in emergence traps.

4.5 Discussion

Populations of *A. bilineata* adults sampled with pitfall traps placed within emergence cages over canola stubble showed abundance curves distinct from those observed with pitfall trap captures in newly seeded canola. Collections from traps within emergence cages indicated discrete periods of peak adult abundance from late June to mid July, but collections from current crop traps were characterized by peak activity periods that did not always fall within such discrete periods, and often did not correspond with peaks observed from the emergence traps (Figures 4.1, 4.4). Such results are not surprising because the two collection strategies sampled different components of the *A. bilineata* population. The emergence traps were sealed to prevent immigration and emigration of the beetles, and the pitfall traps they contained likely removed newly eclosed individuals fairly soon after their emergence. Consequently, these collections would better represent emergence patterns of the species than samples from the current crop pitfall traps. Traps located in the current canola crop would better represent beetle

density as well as seasonal activity, which extended well beyond the periods of emergence in this relatively long-lived species. Colhoun (1953) reported average lifespans of females and males of *A. bilineata* at 46.9 and 48.9 d, respectively, and Fournet et al. (2000) reported a maximum longevity of 126 d. The sustained high levels of activity throughout the season, likely reflecting both immigration from areas outside the plots and the long-lived nature of adults, should enhance the effectiveness of *A. bilineata* as an important predator of *Delia* spp. eggs and larvae, which are also present in canola for much of the season (Griffiths, 1986; Dosdall et al., 1994).

Emergence cages can sometimes result in alterations of soil temperatures within the cages, either by reflection or absorption of incident radiation (Southwood, 1984). However, it is unlikely that the cages used in this study had any such effect or only minor effects because in several previous studies it was found that soil temperatures within and outside the cages were consistently the same at depths of 3 to 5 cm where most root maggot puparia are located (Dosdall, unpublished data).

Collections of *A. bilineata* adults from emergence traps versus traps in open canola plots varied considerably between years. Between-year variation in emergence traps is likely related to host population densities in preceding years. For example, peak captures of *A. bilineata* were approximately three- and five-fold greater in 2003 than in 2004 and 2005, respectively, even with fewer pitfall traps deployed in 2003. Broatch et al. (2006) reported high densities of *D. radicum* in 2002 from the same location, which seems to have been a resource exploited effectively by *A. bilineata*, giving rise to high beetle populations in 2003. The drastic reductions in host populations that occurred in 2003 and 2004, and attributed to drought conditions by Broatch et al. (2006), evidently

caused the reductions in *A. bilineata* densities observed in emergence traps in 2004 and 2005.

Read (1962) found that developmental synchrony between *A. bilineata* and its principal host, *D. radicum*, was temperature dependent. At temperatures of 15.5°C and lower, *D. radicum* developed more rapidly than *A. bilineata*, but at higher temperatures *A. bilineata* emerged before its host. Because adults of *A. bilineata* feed primarily on *Delia* spp. eggs and larvae, emergence preceding its root maggot hosts could be detrimental because of insufficient resource availability for survival of the predator-parasitoid early in the season. In central Alberta, soil temperatures in spring were generally below 15°C (Table 4.1), indicating that emergence of *A. bilineata* should occur later than that of *D. radicum*.

Results indicate that *A. bilineata* required, on average, 458.7 ± 18.8 (S.E.) degree-days and 185.1 ± 2.8 Julian days for emergence of 50% of the population, based on adult captures made within emergence traps. Although no previous determinations of the environmental or developmental factors that affect degree-day requirements for this species seem to exist in the literature, Brunel et al. (1999) reported a requirement of 28.5 d at 17.0°C and 52.1 d at 12.5°C. Based on the developmental threshold of 5.57°C, these would be approximately 326 and 361 degree-days, which are somewhat lower than our estimates for 50% emergence, but suggest that variability in emergence requirements may be influenced by local environmental conditions and/or insect biotype. Host quality can also play a role in *A. bilineata* development (Jonasson, 1994). Developmental time of *A. bilineata* was shown to depend not only on temperature, but also on the weight of the host puparia (Ahlström-Olsson, 1994): the smaller the host puparium, the less time the

parasitoid required to complete its development. Puparia of both *D. radicum* and *D. platura* were common at the study site (Broatch et al., 2006), but puparia of *D. radicum* are approximately three times heavier than those of *D. platura* (Jonasson et al., 1995), so perhaps the early-season pitfall trap captures of *A. bilineata* in our study reflected a population that developed primarily within puparia of *D. platura* and captures later in the season resulted mainly from *A. bilineata* emerging from *D. radicum*.

The phenology of *A. bilineata* is well synchronized with that of *D. radicum*, its principal host in canola agroecosystems in western Canada. Broatch et al. (2006) determined that 50% emergence of the *D. radicum* population occurs at Julian date 170.1 ± 3.5, which corresponds with emergence of 10% of the *A. bilineata* population. At this time (mid June), egg deposition on canola by *D. radicum* is beginning (Dosdall et al., 1994), so some beetles would be available from the onset of root maggot oviposition to exploit this resource. Continued subsequent emergence of *A. bilineata* would continue to cause reductions in *Delia* spp. egg populations, and root maggot larvae could provide a food source for beetles later in the season. Such well synchronized emergence phenologies of *A. bilineata* and its host have not always been observed. For example, Read (1962) found that *A. bilineata* adults emerged after *D. radicum* in Prince Edward Island, and this limited its usefulness for providing root maggot control in brassicaceous crops. In southern Ontario, *A. bilineata* emerged three weeks later than *D. radicum* (Nair and McEwen 1975), an emergence better timed so root maggot eggs and larvae would be available for *A. bilineata*.

Although *D. radicum* is the dominant root maggot species in canola agroecosystems in central Alberta (Griffiths, 1986), *D. platura* can provide an alternate

food source for *A. bilineata* when *D. radicum* populations are low. Unlike *D. radicum* which is univoltine, *D. platura* is bivoltine, with an F_1 generation that has 50% of its population emerging at Julian date 195.8 ± 2.1 (approximately 15 July) (Broatch et al., 2006). High numbers of late-season captures of *A. bilineata* in current crop pitfall traps observed in this study in 2003 and 2005 (Figure 4.4) could be indicative of exploitation of this resource by the predator-parasitoid.

A difference in the timing of emergence based on sex is widespread in insects, with adult males usually eclosing earlier than females (Matsuura, 2006). I found that emergence percentages were equivalent for males and females throughout their emergence period (Figure 4.3). When protandry occurs, it usually serves as a reproductive adaptation to maximize the number of encounters with females (Wiklund and Solbreck, 1982), but in a relatively long-lived species like *A. bilineata* the frequency of such encounters for mating may not be limiting.

Although I found that periods of emergence and activity of *A. bilineata* are well synchronized for the species to attack various life stages of its root maggot hosts in canola, *D. radicum* and *D. platura* remain significant pests of the crop in western Canada, capable of causing enormous crop losses annually (Soroka et al., 2004). Current crop management practices may be partly responsible for less than optimal biological control of *Delia* spp. in this system. For example, early-season applications of herbicide are routinely made to control weeds, fungicide can be applied at flowering thus reduce disease infestations, and insecticide applied as a seed treatment to control flea beetle herbivory can be followed later in the season by foliar insecticide to reduce populations of crop herbivores (Thomas, 2002). Several studies have identified the risks posed by

these pesticides to biocontrol agents like *A. bilineata*. For example, Cox (1999) reported that the herbicide 2,4-D amine killed over 50% of *A. bilineata* adults in one study, and this herbicide or others in the same chemical group are commonly used to treat volunteer weeds in canola stubble where most *A. bilineata* adults emerge (Brook, 2006). In addition, synthetic pyrethroid insecticides had a negative influence on oviposition by *A. bilineata* under laboratory conditions (Samsoe-Petersen, 1985), and products from this chemical family are registered for use in the crop to treat various insect pest species. Several studies have identified cultural practices that can reduce canola crop losses from root maggots (e.g., Dosdall et al., 1996a, 1996b, 1998), but to date no research has been conducted to identify cultural strategies that can enhance populations of their natural enemies. By optimizing cultural conditions that favor development of *A. bilineata* populations, and by also incorporating integrated management practices for weeds that are less reliant on herbicide applications like those proposed by Harker et al. (2005), it is likely that chemical pesticide applications can be reduced in this crop and populations of beneficial species like *A. bilineata* can be enhanced. This determination of temporal patterns of emergence and activity of *A. bilineata* can promote natural enemy conservation by enabling growers to adjust crop planting dates and scheduling weed or pest control options to optimize root maggot control by its principal natural enemy.

My study emphasizes the importance of using combined trapping methods to obtain descriptions of both emergence and current crop activity density in this system. Used in isolation, a particular trapping method would reflect only emergence or activity density, and could result in misleading interpretations of population dynamics. The recommended rotational regime in this cropping system is to grow canola on a site only

once every three to four years (Thomas, 2002), so the majority of the *A. bilineata* population in a particular field would arise from immigration from areas seeded to canola in the preceding year. Activity density levels assessed in pitfall trap collections in these situations likely reflect the proximity of canola fields from the preceding year, the population densities of the root maggots and *A. bilineata* in those fields, and interactions among members of the predatory guild, but further research is needed to confirm those relationships. In addition to differences between years in numbers of *A. bilineata* emerging from canola stubble, I found that current crop captures of *A. bilineata* in late June (reflecting the activity density component of the capture data) were much higher in 2004 than in 2005 even though early season captures of *A. bilineata* in 2005 were initially high. Reasons for this between-year variance are unclear, but it could reflect higher immigration from areas outside the study site, or interactions among *A. bilineata* and other insect species in the agroecosystem. A recent review of empirical studies documenting trait-mediated indirect interactions in food webs indicates that these effects are important to community dynamics (Werner and Peacor, 2003). Prasad and Snyder (2006) found that the presence of the large carabid beetle, *Pterostichus melanarius* (Illiger), reduced activity-densities of small beetles like *A. bilineata* not by changing the densities, but rather by influencing activities of the smaller species and thus, their overall abundances in trap captures. *Pterostichus melanarius* was present in the current crop pitfall collections in each year of our study, but it was particularly abundant in 2005 when its numbers increased seven-fold over those in 2004 and peaked during Julian weeks 25 - 27 (J. Broatch, unpublished data). Lower than expected *A. bilineata* collections during those Julian weeks in 2005 could reflect reduced *A. bilineata* activity in response to

heightened activity of *P. melanarius*. Such interactions among members of the predator guild would affect estimates of degree-day and Julian date requirements for emergence based on the current crop captures. Trait-mediated indirect interactions can have a significant impact on ecosystem structure and function, but such dynamics remain to be investigated in canola agroecosystems.

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Table 4.1: Mean monthly soil temperature data (°C), mean low and high daily soil temperatures, mean monthly air temperatures and long-term normal air temperature values during the growing seasons at Lacombe, AB from 2003 to 2005.

Year	Monthly soil mean	Low/high daily soil mean	Monthly air mean	1908-2005 Mean °C
2003				
April	3.07	0.05/7.53	3.7	3.7
May	7.88	1.57/13.88	8.7	9.8
June	14.27	11.33/18.36	14.2	13.6
July	17.76	14.78/20.00	16.9	16.1
August	17.42	14.16/19.41	17.1	14.9
2004				
April	5.25	1.90/9.83	5.5	3.7
May	9.66	5.33/13.03	7.9	9.8
June	15.00	11.67/19.45	13.0	13.6
July	17.35	15.52/20.68	15.9	16.1
August	16.30	12.33/19.29	14.2	14.9
2005				
April	4.92	0.33/10.15	5.7	3.7
May	11.20	3.74/15.23	10.3	9.8
June	14.44	11.53/18.60	12.8	13.6
July	17.69	15.68/20.00	15.6	16.1
August	14.41	10.05/18.15	13.1	14.9

Table 4.2: Estimates for degree-day and Julian day requirements for 10, 25, 50, 75, and 95% emergence of *Aleochara bilineata* adults based on logistic analysis of adult collections from 2003 to 2005 in pitfall traps in enclosed emergence cages and in the current canola crop. In 2003 and 2005, estimates were performed with non-logistic, linear analysis for pitfall trap captures of beetles in open canola plots.

Year/generation	% Emergence	Degree-days (soil base 5.57°C)	Julian date
	10	334.88	178.50
2003	25	381.83	182.88
Emergence trap sampling	50	428.44	187.21
	75	475.61	191.57
	95	563.17	199.41
	10	215.04	167.67
2003	25	334.56	177.83
Current crop sampling	50	533.76	194.76
(with linear analysis)	75	732.96	211.69
	95	892.32	225.23
	10	381.42	171.61
2004	25	432.09	180.39
Emergence trap sampling	50	493.22	188.60
	75	571.50	195.97
	95	Not obtained	204.50
	10	93.32	159.68
2004	25	270.69	170.58
Current crop sampling	50	379.11	179.55
	75	469.77	187.99
	95	578.58	201.46
	10	300.24	165.35
2005	25	376.67	172.28
Emergence trap sampling	50	454.58	179.56
	75	532.02	186.88
	95	653.06	198.42
	10	117.43	144.13
2005	25	283.00	159.79
Current crop sampling	50	558.93	185.89
(with linear analysis)	75	834.87	211.98
	95	1055.62	232.86

Table 4.3: Ordinary least squares parameter estimates (±S.E.) resulting from logistic or linear (where noted with just *a*, *b*) analysis of *Aleochara bilineata* adults from either emergence trap or current crop sampling from 2003 to 2005.

Year/generation	Logistic model parameter [a]	Degree-days (± S.E) (soil base 5.57°C)	Julian date (± S.E.)
2003	*a*	0.34 ± 0.50	0.41 ± 0.48
Emergence pitfall trap	*c*	98.36 ± 0.81	98.66 ± 0.80
	b	0.02 ± 0.00	0.26 ± 0.01
	m	427.63 ± 1.99	187.17± 0.18
	adjusted r^2	0.99	0.99
2003	*a*	-16.99 ± 2.25	-237.62 ± 11.14
Current year pitfall trap	*b*	0.13 ± 0.00	1.48 ± 0.06
	r^2	0.99	0.99
2004	*a*	-4.42 ± 4.81	-0.02 ± 5.97
Emergence pitfall trap	*c*	92.84 ± 12.66	80.52 ± 9.87
	b	0.018 ± 0.01	0.54 ± 3.84
	m	474.14 ± 75.31	178.97 ± 14.11
	adjusted r^2	0.89	0.85
2004	*a*	7.26 ± 6.25	4.10 ± 4.71
Current year pitfall trap	*c*	99.57 ± 7.64	96.38 ± 6.20
	b	0.01 ± 0.00	0.13 ± 0.02
	m	403.94 ± 19.32	180.27 ±1.55
	adjusted r^2	0.98	0.98
2005	*a*	-0.68 ± 2.13	-1.60 ± 2.39
Emergence pitfall trap	*c*	101.90 ± 4.50	102.73 ± 5.92
	b	0.01 ± 0.00	0.15 ± 0.03
	m	455.34 ± 10.92	179.49 ± 1.32
	adjusted r^2	0.99	0.98
2005	*a*	-0.21 ± 4.87	-128.06 ± 12.63
Current year pitfall trap	*b*	0.09 ± 0.01	0.96 ± 0.07
	R^2	0.92	0.94

[a] Data were fitted to Equations 4.1 or 4.2 (see text). *b* is the slope, *m* is the point of inflexion, *c* and *a* are asymptote parameters (equation 4.2)

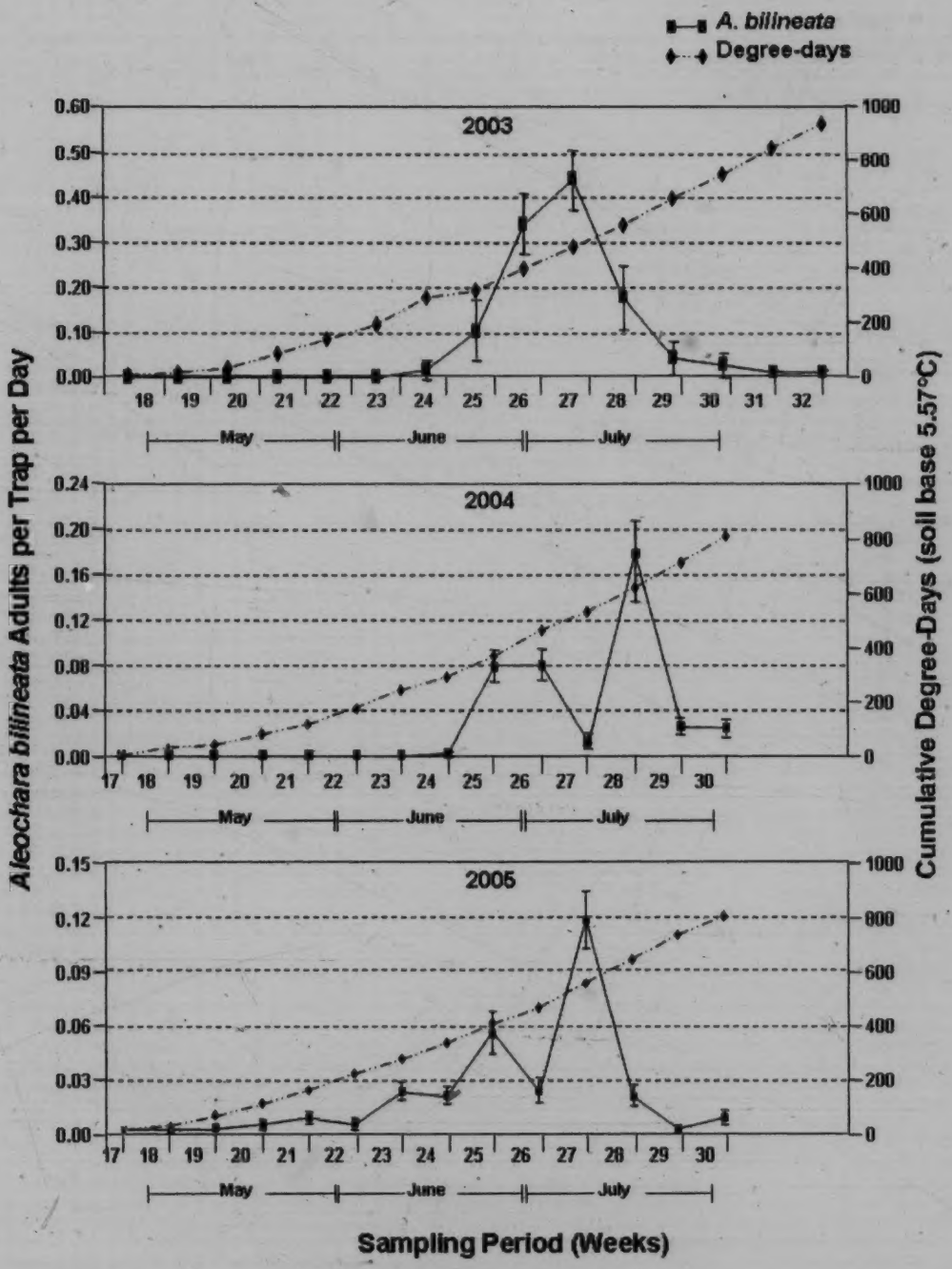

Figure 4.1: *Aleochara bilineata* adult captures per pitfall trap per day (± S.E.) within emergence traps in canola stubble compared with cumulative degree-days based on a 5.57°C soil developmental threshold requirement over three field seasons (2003-2005). Sampling periods are given in Julian weeks throughout the season.

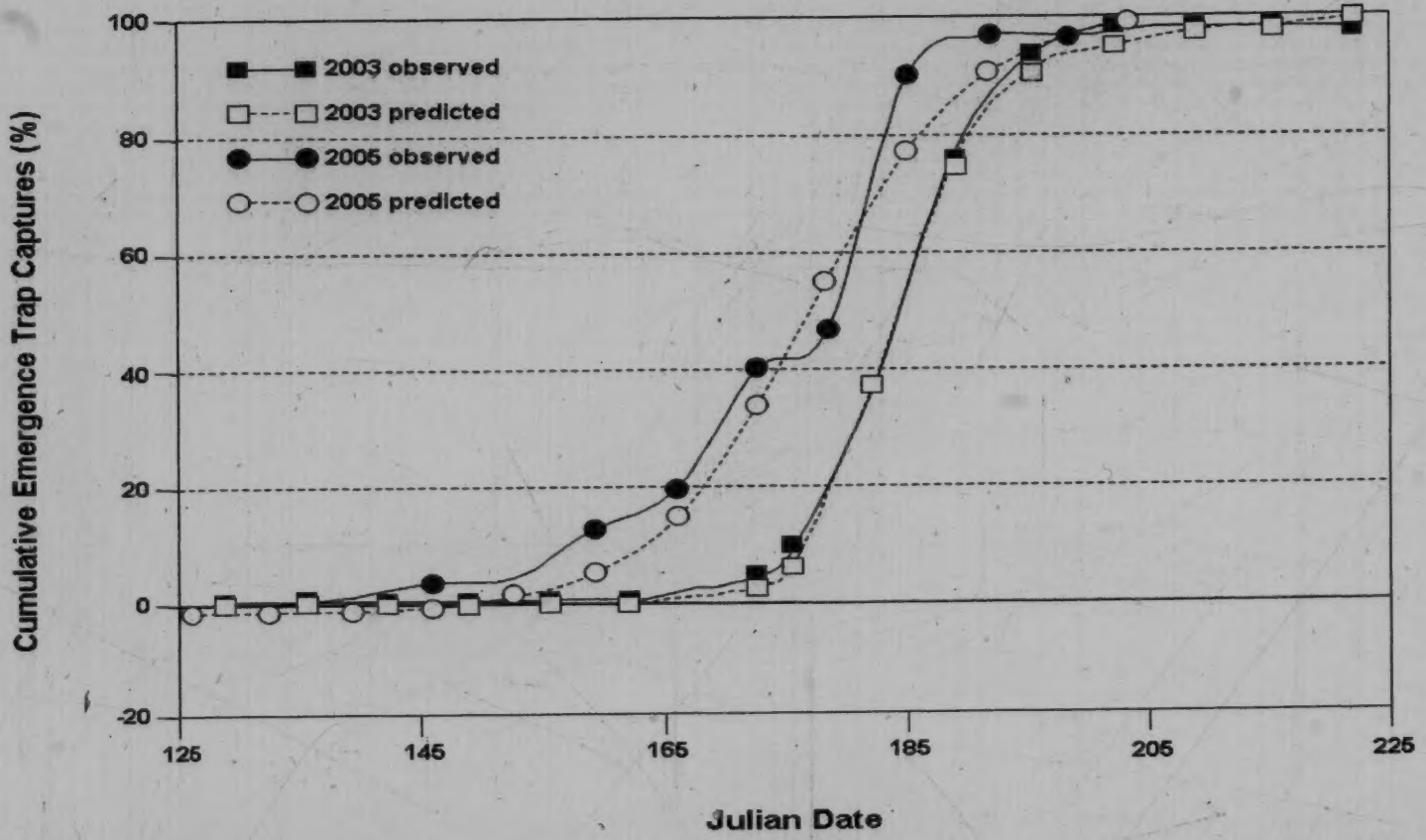

Figure 4.2: Observed cumulative emergence patterns and patterns predicted with logistic analysis for *Aleochara bilineata* during 2003 and 2005 in canola in Lacombe, AB.

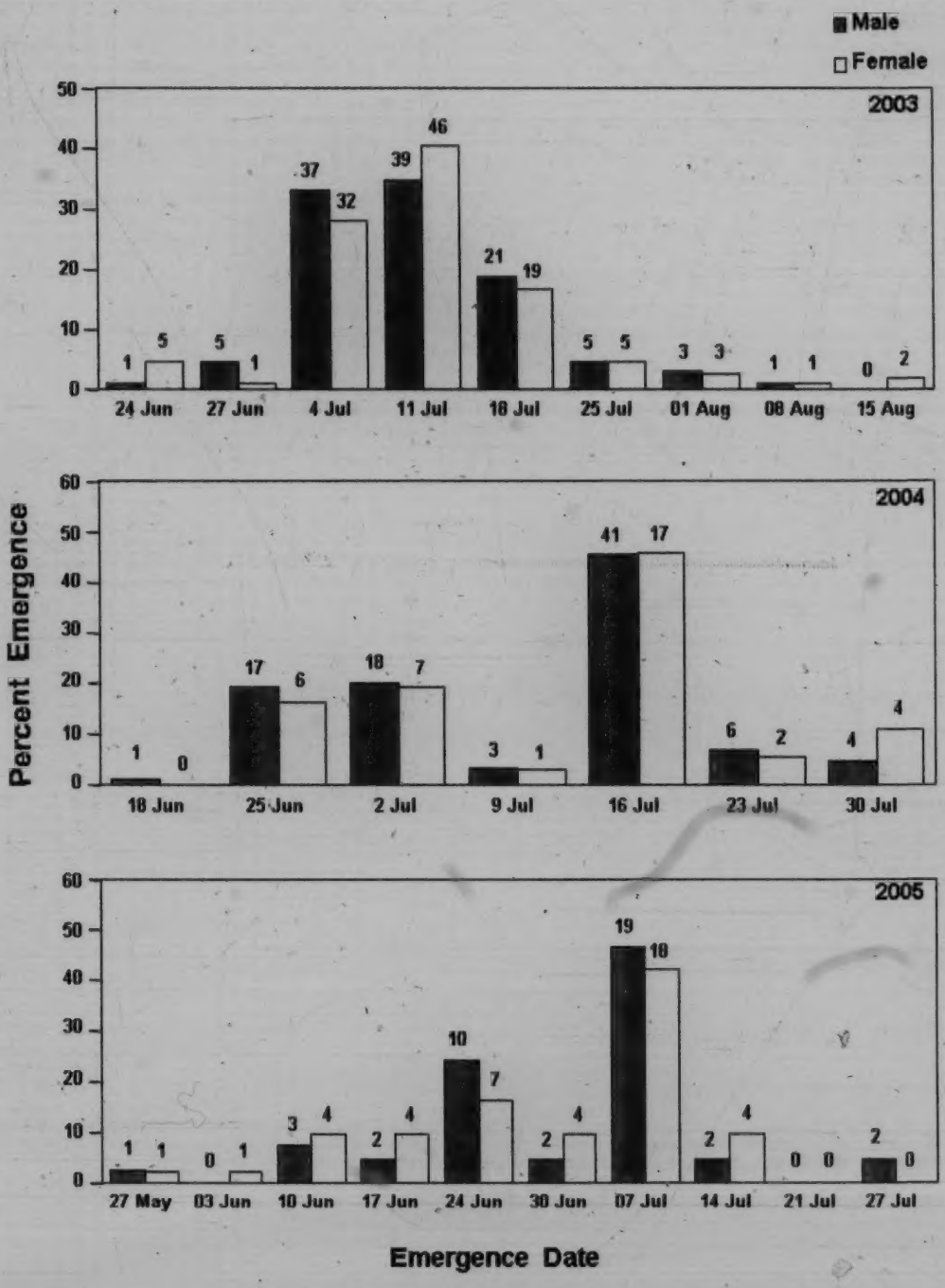

Figure 4.3: Percentage emergence of *Aleochara bilineata* males and females captured in pitfall traps within emergence cages located on canola stubble over three seasons (2003-2005). Numbers on histograms give total specimens of males and females collected on each date when emergence captures were recorded.

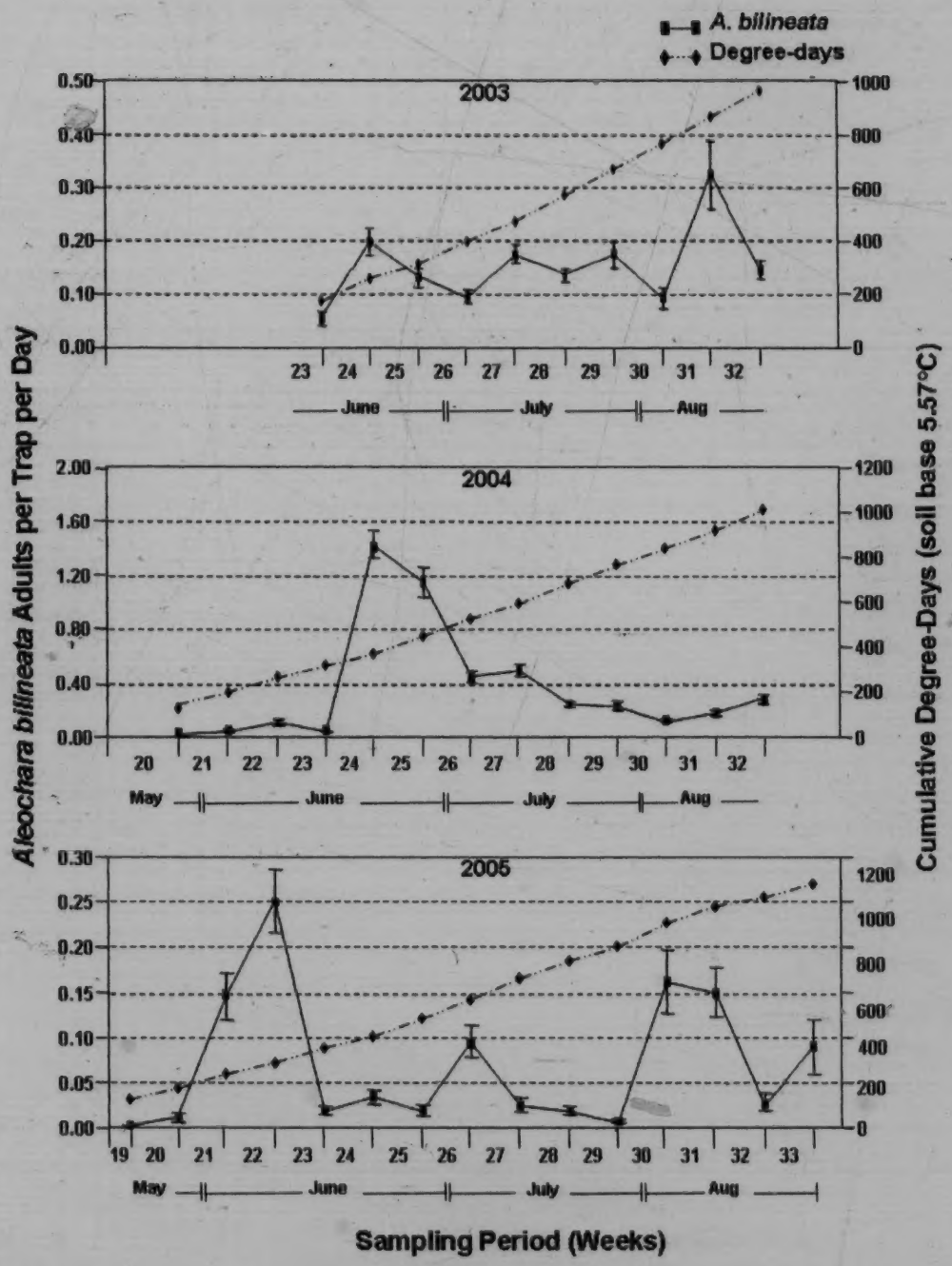

Figure 4.4: *Aleochara bilineata* adult captures per pitfall trap per day (± S.E.) in current canola crop sampling compared with cumulative degree-days based on a 5.57°C soil developmental threshold requirement over three field seasons (2003-2005). Sampling periods are given in Julian weeks throughout the season.

Chapter 5: Responses of Carabid and Staphylinid Species Assemblages to Weed Biomass and Canola Species

5.1 Abstract

Habitat management through increasing plant biodiversity is known to affect insect populations, both herbivores and their natural enemies. An important effect of greater plant heterogeneity could be to provide environments that promote or enhance biological control, through increased abundance of predatory and parasitoid populations, and so reduce dependence on pesticides. Field studies were conducted during 2003 to 2005 at Lacombe, AB, Canada to manipulate weed populations in both species of canola, *Brassica rapa* L. and *Brassica napus* L., to investigate responses among selected species of natural enemies. Significant responses were observed among several predaceous species of Carabidae and Staphylinidae. As weed biomass declined, the activity density of the root maggot (*Delia* spp.; Diptera: Anthomyiidae) predator-parasitoid *Aleochara bilineata* Gyllenhal (Coleoptera: Staphylinidae) increased ($P < 0.01$). Carabid community structure was influenced by certain canola species and weed biomass. Significant preferences for canola species were found among several predaceous carabid beetles, including *Amara littoralis* Mannerheim, *Amara farcta* Leconte, and *Pterostichus melanarius* (Illiger), and the staphylind beetle *A. bilineata*. Effects of varying weed populations and canola species on carabid and staphylinid assemblages are complex and require species-specific evaluations and analysis.

5.2 Introduction

In the Northern Great Plains of North America, canola (*Brassica napus* L. and *B. rapa* L.) is routinely grown in systems that strive to produce weed-free monocultures (Thomas, 2002). However, increasing plant biodiversity in agroecosystems has the potential to reduce the abundance and economic damage of herbivore pests (Altieri and Letourneau, 1984). Altering crop monocultures by enhancing plant biodiversity can increase the variability in microclimatic conditions within crop canopies. For example, increased plant biodiversity can alter levels of humidity and light penetration, and so increase the availability of protective refugia for predators and parasitoids of herbivore pests (Landis et al., 2005; Pavuk et al., 1997). One strategy for increasing plant biodiversity in annual crops is to tolerate small populations of weeds (Marshall et al., 2003), and genetically modified herbicide-tolerant crops provide an opportunity for manipulating weed populations to enhance their beneficial effects without compromising yield (Dewar et al., 2003).

Root flies or root maggots (*Delia* spp., Diptera: Anthomyiidae) are chronic and serious pests of canola in western Canada, particularly in vast areas of cropland throughout northern and central Alberta and in the Aspen Parkland Ecoregion of Saskatchewan and Manitoba (Soroka et al., 2004). Damage is caused by larvae feeding on canola taproots, and this can lead to reductions in root weight and root sugar content, stunted growth, premature lodging, decreased raceme numbers, and decreased seed yields (McDonald and Sears, 1991; Griffiths, 1991; Hopkins et al., 1999). Invasion of injured roots by root rot fungi (*Fusarium* spp.) can cause further yield reductions (Griffiths, 1986a, 1986b). Five root fly species occur in canola, but most damage is inflicted by the

cabbage maggot, *Delia radicum* (L.), the turnip maggot, *Delia floralis* (Fallén), and the seedcorn maggot, *Delia platura* (Meigen) (Liu and Butts, 1981; Griffiths, 1986a, 1986b; Broatch et al., 2006). Root maggot infestations have become major constraints in canola production, responsible for yield losses estimated as high as $100 million (CAD) annually (Soroka et al., 2004).

The principal natural enemies of root maggots include species of Staphylinidae and Carabidae (Coleoptera). Among Staphylinidae, the predator-parasitoid *Aleochara bilineata* Gyllenhal is the dominant root maggot natural enemy in canola in western Canada (Turnock et al., 1995; Hemachandra, 2004). Adults of *A. bilineata* are voracious predators of *D. radicum* eggs and larvae. Read (1962) concluded that under optimum conditions a single pair of *A. bilineata* adults could destroy approximately 1,210 eggs and 128 larvae in their lifetimes. Each *A. bilineata* female can produce approximately 9 to 15 eggs per day or 700 eggs in its lifetime (Colhoun, 1953; Fournet et al., 2000). Larvae of *A. bilineata* hatch in 3 to 7 d, and first instars locate root maggot puparia. After chewing an opening in the puparial wall, the larva consumes the developing root maggot pupa within (Royer et al., 1998). Overwintering of *A. bilineata* occurs as a first instar within the puparium, and new generation adults emerge in the following spring (Colhoun, 1953).

Several species of Carabidae have been associated with root maggot predation. Treherne (1915) documented *Amara farcta* Leconte feeding on *D. radicum* eggs and larvae in British Columbia. Wishart et al. (1956) found that in Ontario *Bembidion quadrimaculatum oppositum* Say was the most abundant and effective predator of *D. radicum* eggs, and another carabid, *Bembidion nitidum* Kirby, was also highly predatory on eggs (Wishart et al., 1956). When exclusion techniques reduced carabid populations

by an estimated 72%, *D. radicum* egg survival increased by 50% (Wright et al., 1960). Similarly, a decrease of *B. quadrimaculatum* populations by 44% was associated with a 55% increase in egg numbers in the U.S.A. (Pitre, 1965), and in Ireland 59% fewer carabids resulted in a 52% increase in *D. radicum* egg numbers (Ryan and Ryan, 1980). When carabid numbers were lowered by insecticide applications, *D. radicum* egg numbers increased (Coaker, 1966).

The abundance and activity of ground beetles is influenced by vegetational background. Norris and Kogan (2000) noted that higher ground beetle numbers were associated with weedy situations, and they identified plant cover as a factor responsible for increased activity of the predators. Even vegetation in surrounding fields, hedges, and tree rows can influence the carabid fauna in agroecosystems, including species sensitive to agricultural practices (Hance et al., 1990). Recent studies determined that in canola weedy backgrounds, or populations of weeds in densities sufficiently low that minimal interspecific crop competition occurred, were associated with reduced infestations of *Delia* spp., presumably because weeds interfered with the sequence of behaviors required by females during oviposition (Finch and Collier, 2000; Dosdall et al., 2003; Broatch et al., 2008). However, the influences of weeds on populations of root maggot natural enemies, including Carabidae and the staphylinid beetle *A. bilineata*, have never been investigated previously in canola agroecoystems, and the diversity of microhabitats that weeds create has the potential to enhance biological pest control. The objective of this study was to vary herbicide application rates in canola to manipulate weed populations, and so test the hypothesis that carabid and staphylinid abundances increase with greater ecosystem heterogeneity.

5.3 Materials and Methods

5.3.1 The Study Site and Experimental Design

The study was conducted during 2003, 2004, and 2005 at the Agriculture and Agri-Food Canada Research Station, Lacombe, AB (113°44′W; 52°28′N). Soils at the site developed on glacial lacustrine deposited material (Bowser and Peters, 1951). Plots seeded to canola were on black Chernozemic clay loam soil (43% sand, 21% silt, and 36% clay) with a pH of 5.9 and 8.2% organic matter content.

The experiment was a randomized complete block design with four replications involving factorial combinations of six herbicide application rates and two canola species. Plots of *B. napus* (cv. InVigor 2733) and *B. rapa* (cv. Hysyn 110) were seeded on 2 May 2003, 17 May 2004, and 10 May 2005 and were fertilized at 100% of the soil test recommendations for canola production. Plots measured 8 by 15 m and were seeded into cereal stubble with a ConservaPak® drill with 30.5 cm row spacings and at a density of 150 seeds m^{-2}. Seed was treated with Helix® (containing 10.3% thiamethoxam, 1.24% difenoconazole, 0.39% metalaxyl-M, and 0.135 fludioxonil) at the manufacturer's recommended rate to reduce herbivory to seedlings by flea beetles (*Phyllotreta* spp.) (Coleoptera: Chrysomelidae). To simulate natural weed populations, tame oat (*Avena sativa* L.) was seeded at 100 seeds m^{-2} perpendicular to the canola seed rows. Plots were separated within the blocks by 2 m of bare soil, and between blocks by a 15-m strip seeded to winter wheat (*Triticum aestivum* L.). Dicotyledonous weeds were removed from the plots through applications of Muster® (ethametsulfuron-methyl) and Lontrel®

(clopyralid) applied in-crop at 22 g a.i. ha^{-1} and 150 g a.i. ha^{-1}, respectively. Herbicide rates for monocotyledonous weeds involved sethoxydim applied at 0, 20, 40, 60, 80, and 100% of the label rate of 200 g a.i. ha^{-1} in 2003 and at 0, 5, 10, 20, 40, and 100% of the label rate in 2004 and 2005 when canola was in the two- to three-leaf stage of development. Herbicides were applied in 110 L ha^{-1} of water at 275 kPa using a sprayer equipped with flat-fan nozzles.

Weed densities were determined for each plot approximately 48 h before and 20 d after the sethoxydim applications. All weed counts were obtained from four 0.5 m^2 quadrats positioned diagonally across each plot. Population counts (plants m^{-2}) of monocotyledonous and dicotyledonous weeds were conducted concurrently, with weeds identified to species and their growth stages recorded. Biomass of weeds (kg ha^{-1}) was determined four weeks after spraying from within the same four quadrats where the original pre-spray counts were performed. Weeds were cut off at the root-stem interface, sorted by type (monocot or dicot), bagged, labeled, and dried at 60°C for 2 d before being weighed.

5.3.2 Insect Sampling Protocol

Pitfall traps were used each year to investigate activity dynamics of field populations of *A. bilineata* and Carabidae. One pitfall trap per plot was established in the newly seeded canola plots in 2003, but two traps per plot were used in 2004 and 2005. Traps were established on 29 April 2003, 23 April 2004, and 22 April 2005. They were placed randomly within the plots, except that they were at least 2 m in from the plot edges. Pitfall traps consisted of two GenPak® plastic cups, placed one inside the other.

The bottom cup was placed into a hole 15 cm deep and 11 cm in diameter so the cup was at ground level. The second cup was placed within the first and the rim cut so that only a 2.5 by 2.5 cm tab remained above the soil surface. The second cup was labeled as to the plot identification and its location in either the front or rear of the plot. A 17 by 17 cm rain cap was placed about 5 cm above each trap. Pitfall traps were filled to a 5-cm depth with propylene glycol.

Pitfall trap collection and replacement occurred weekly. The inner sleeve components of the traps were removed from the field and taken to the laboratory for processing. There the trap contents were labeled as to collection date, plot number, and within-plot location and placed into 70% alcohol until specimens could later be sorted, identified, and data recorded.

5.3.3 Species Identifications and Voucher Specimens

Identifications of *A. bilineata* specimens were performed using Klimaszewski (1984) with representative species identifications verified by J. Klimaszewski (personal communication). Carabids were identified to species using the keys of Lindroth (1969) and a reference collection from Agriculture and Agri-Food Canada in Lethbridge. Species that could not be distinguished morphologically were combined for analysis: the group *Amara torrida* (Panzer) also included *Amara lacustris* LeConte and *Amara carrinata* Leconte. Species identifications of representative specimens were verified by G.E. Ball (personal communication). Voucher specimens from the study have been deposited in the Strickland Museum of Entomology, University of Alberta, Edmonton, AB and at the Agriculture and Agri-Food Canada Research Centre in Lacombe, AB.

5.3.4 Data Analysis

5.3.4.1 Regression Analysis

The relationships between weed dry weight (independent variable) and activity densities of *A. bilineata* and Carabidae (dependent variable) were investigated using linear regression analysis (PROC GLM, ESTIMATE option) (SAS Institute Inc., 2004). Data were fitted to the linear model:

$$Y = a + bX \qquad [5.1]$$

where Y is the beetle activity density, X is the weed biomass, a is the Y intercept, and b is an estimated regression coefficient. All data were transformed, $\log_{10}(x+1)$, prior to analysis to stabilize variances in the samples and to meet the assumption of homoscedasticity for regression analysis.

5.3.4.2 Ordination Analysis

Ordination was used to extract the dominant patterns in species composition of *A. bilineata* and Carabidae collected in pitfall traps from an infinite number of possible patterns (McCune and Grace, 2002). Ordination diagrams were used to plot synthetic axes against one another, so that the distances between points in the ordination were approximately proportional to the dissimilarities between the entities (McCune and Grace, 2002). Distinct symbols were selected to show the herbicide or canola species treatments, and in some figures different-sized symbols proportional to the magnitude of the variable were employed to display patterns in the data.

Before analyzing species composition and activity density, the two trap catches for each species on every sampling date in each plot were combined and standardized by dividing the sum by the total number of trap days:

Plot X = (Carabids A + Carabids B) / (Days A + Days B) [5.2]

where A and B were pitfall traps within the same experimental plot. This procedure allowed standardizing catch rate for the occasional non-operational trap. Furthermore, the catch rates for all sampling dates were combined for each plot to obtain a total catch rate for the year.

Non-metric multidimensional scaling (NMS) analysis was performed to compare the species composition of beetle assemblages characterizing each treatment. In a NMS ordination plot, the distance between data points is directly proportional to species compositional dissimilarity (McCune and Grace, 2002). Sorensen (Bray-Curtis) distances were used to measure the dissimilarity matrix between samples. Starting coordinates were selected randomly. Forty runs with a maximum of 400 iterations were performed using real data. This process was initially conducted with six dimensions, but in each subsequent cycle it was reduced by one dimension. The best dimension was selected using a Scree Plot and considering the dimension beyond which additional dimensions provided only small reductions in stress, or represented the "elbow" area of the Scree Plot (McCune and Grace, 2002). In NMS, the stress measures the distortion between the positions of real data points from the data presented graphically. Therefore low stress represents few distortions from the real position of the data points and is associated with a graphic that more accurately represents the dissimilarities in species composition than high stress. A preferred number of dimensions is suggested when

adding an axis does not reduce stress by more than five. A Monte Carlo probability was then calculated to evaluate whether the final stress was lower than 95% of 50 runs with randomized data. Species vectors were calculated using a minimum r^2 of 0.3 and overlaid on the final ordination. The length and angle of the vector are an indication of the strength and direction of the species association, respectively.

5.3.4.3 Indicator Species Analysis

Indicator Species Analysis was performed using PC-Ord (McCune and Mefford, 1999) to identify associations between carabid species and herbicide treatment or crop variety. Indicator Species Analysis is most useful for detecting and describing the value of different species for indicating environmental conditions. Indicator Species Analysis evaluates the relative frequency and relative catch of a single species and compares this among the predefined treatments. A perfect indicator of a particular group would be faithful to or always present in that group. The result is then compared with a randomly achieved value using a Monte-Carlo probability test. An indicator measure ranging from 0 (poor indicator) to 100 (good indicator) is then calculated with an associated *P* value from the Monte-Carlo test. Indicator Species Analysis is a natural companion analysis to multi-response permutation procedures, supplementing the test of no multivariate difference between groups with a description of how well each species separates among groups (McCune and Grace, 2002).

5.3.4.4 Multi-response Permutation Procedures

Multi-response permutation procedure (MRPP) is the non-parametric equivalent of MANOVA, and a procedure for testing the hypothesis of no difference between two or more groups (McCune and Grace, 2002); it is performed in PC-ORD (McCune and Mefford, 1999). MRPP has the advantage of not requiring distributional assumptions such as multivariate normality and homogeneity of variances. MRPP provides a test statistic, a measure of "effect size" and a *P*-value. The test statistic, *T*, describes the separation between groups. The more negative the *T* value, the stronger the separation. The test statistic is the difference between the observed and expected deltas (the weighted mean within-group distance) divided by the square root of the variance in delta. It is similar to Student's T-test. In this study a Sorensen (Bray-Curtis) distance measure was used.

The effect size that is independent of the sample size is given by *A*, or the chance-corrected within-group agreement. This agreement statistic, *A*, describes within-group homogeneity compared to the random expectation. When all items are identical within groups, the observed delta = 0 and *A* = 1 (which is the highest value for *A*). In community ecology, values for *A* are commonly below 0.1, and a value of *A* greater than 0.3 is fairly high (McCune and Grace, 2002). MRPP uses Sorensen (Bray-Curtis) distances to calculate the variation within (*A* value) and between groups (*T* value), and evaluates the probability that these groups are similar (McCune and Grace, 2002). Sorensen distances are less prone than Euclidean distances to exaggerate the influence of outliers in the data.

5.3.4.5 *Aleochara bilineata* Activity Density

Aleochara bilineata catch data were transformed, $\log_{10}(x+1)$, prior to statistical analysis. The assumptions of normal distribution and equal variance for parametric analyses were met after transformation. To investigate the effect of the treatment on activity density of total *A. bilineata* captures, an ANOVA with canola species (*B. rapa* and *B. napus*) and weed dry weight $\log_{10}(x+1)$ as factors was performed for total captures for the entire study with PROC MIXED (SAS Institute Inc., 2004). Block, year and canola species were used as fixed factors to remove variability that may be attributed to site, and transformed weed dry weight data were used as a covariate.

5.4 Results

5.4.1 Staphylinid and Carabid Fauna and Seasonal Activity

A total of 4,100 specimens of *A. bilineata* were collected in the pitfall traps from 2003 to 2005 inclusive. *Aleochara bilineata* was the most abundant staphylinid species in the samples, but other species collected from this family included *Aleochara verna* Say, *Dinaraea angustula* (Gyllenhal), *Philhygra subpolaris* (Fenyes), *Philonthus occidentalis* Horn, *Oxypoda robusticornis* Bernhauer, *Mocyta fungi* (Gravenhorst), *Mycetoporus lucidulus* LeConte, *Philhygra* sp., and *Lathrobium* sp. A lack of taxonomic keys for this family in western Canada precluded construction of a comprehensive staphylinid species list. Seasonal activity density patterns of *A. bilineata* have been reported elsewhere (see Chapter 4).

A total of 14,025 carabid beetles representing 59 species in 19 genera were collected during 2003 to 2005 (Table A5.1). The 10 most abundant species captured over the three seasons represented 94.5% of total captures. Those species were *Pterostichus*

melanarius (Illiger) (56.7%), *Agonum placidum* (Say) (8.9%), *Amara torrida* (Panzer) (5.1%), *Clivina fosser* L. (5.4%), *Amara quenseli* (Schönherr) (4.7%), *Amara littoralis* Mannerheim (4.2%), *Carabus granulatus* L. (2.9%), *Agonum cupreum* Dejean (2.1%), *Bembidion rupicola* Kirby (1.5%), and *Pterostichus adstrictus* Eschscholtz (1.9%). Thirty species were represented by 10 or fewer specimens (Table A5.1).

Considerable variation was observed between years in total trap captures of Carabidae, and in the species composition of the pitfall trap collections. For example, more carabids were found in pitfall trap collections in 2005 (8,035) than in 2003 (1,481) and 2004 (4,509) (Table A5.1). In 2003, only 85 specimens of *P. melanarius* were collected in the traps and this species accounted for about 6% of all trap captures. In 2004 and 2005, however, 1,473 and 6,395 specimens of the same species were collected, respectively, representing approximately 33 and 80% of all carabids collected in those years. In 2003, *C. granulatus* represented 21% of all carabids captured and was the dominant species in the collections, but it accounted for only 0.02 and 1.20% of all beetles captured in 2004 and 2005, respectively.

Pitfall trap collections of *P. melanarius* greatly exceeded those of any other species at the study site when beetle numbers were totaled over all years of study. Activity density of *P. melanarius* was comparatively low from mid May to mid June, but trap captures increased rapidly thereafter to a peak of activity in late June when approximately 1,300 beetles were collected (Figure 5.1a). Trap captures declined during the next month to late July, but then increased to a second, smaller peak of activity density in early August. By mid August trap captures of *P. melanarius* had declined to levels similar to those observed in mid May. Pitfall trap collections of *A. placidum* were

low until late June, but then increased rapidly over the next two weeks to reach an activity density maximum in early July when a total of approximately 430 beetles were collected (Figure 5.1b). Populations then declined rapidly over the next three weeks to levels near zero. Trap captures of *A. littoralis* remained low until mid June, but then increased to a maximum in late June to early July (Figure 5.1c). Activity density levels declined gradually over the next three weeks, and remained low for the remainder of the season. Greatest activity of *B. rupicola* was observed early in the season, from mid May to mid July, but thereafter few specimens were collected in pitfall traps (Figure 5.1d). Similarly, *C. fossor* was most abundant in pitfall trap captures early in the season, from mid May to late June, but was found in very low numbers for the remainder of the season (Figure 5.1e). Very few specimens of *A. quenseli* were collected in pitfall traps until late July, and greatest activity density levels were observed for the following three weeks until activity density declined to low levels at the end of August (Figure 5.1f).

5.4.2 Relationship of *A. bilineata* Activity Density and Weed Dry Weight

Pitfall trap captures of *A. bilineata* were significantly more abundant in plots of *B. rapa* than in *B. napus* in all three years ($F = 10.41$, df = 5, 15, $P < 0.01$). Covariate analysis determined that *A. bilineata* captures were also significantly, but negatively, correlated with weed dry weight ($F = 3.25$, df = 6, 114, $P < 0.01$).

A negative linear relationship was observed between monocotyledonous weed dry weight and *A. bilineata* activity density in 2003 and 2004. This relationship was significant statistically ($P < 0.05$) except for plots of *B. napus* in 2003, and for both canola species in 2005 (Table 5.1). However, the relationship was highly significant

when data for each canola species were combined for the three years of study, and when data for the two canola species were grouped for all years of study ($P < 0.001$) (Table 5.1; Figure 5.2).

No significant relationship was observed between dicotyledonous weed dry weight and *A. bilineata* activity density in any individual crop species or year ($P > 0.05$) (Table 5.1). However, when data were combined for all three years of the study, a significant negative linear relationship was observed for both *B. rapa* ($P < 0.001$) and *B. napus* ($P < 0.012$) (Figure 5.3). When activity density values were combined for both canola species over all years of the study, this relationship was also highly significant statistically ($P < 0.001$) (Table 5.1) (Figure 5.3).

5.4.4 Beetle Community Patterns in Relation to Herbicide Treatment and Canola Species

In 2003, the best fit in the NMS analysis was a two-dimensional plot (stress = 20.304; Monte Carlo Randomization Test $P = 0.048$). The r^2 values for axes 1.and 2 were 0.384 and 0.406 respectively, explaining 79% of the variance in the data. Two dimensions provided the best reduction in stress in the Scree Plot analysis. Vectors representing *A. bilineata* ($r^2 = 0.600$) were generally directed toward treatments where herbicide was applied at 20 to 80% of the label rate, while the vector for abundance of *C. granulatus* ($r^2 = 0.300$) was not pointed in a reliable direction in relation to any treatment, but it did seem to favor *B. napus* over *B. rapa* (Figure 5.6).

MRPP analysis to determine the importance of canola species for governing beetle species assemblages was significant (T = -4.324, A = 0.050, P < 0.001) (Table 5.2). Herbicide treatment did not have a significant effect on carabid species composition.

Carabus granulatus favored the quadrant occupied primarily by *B. napus* in the ordination graph (Figure 5.6), an observation supported by the Indicator Species Analysis. The indicator species value of 63.8 was significant (P = 0.049) (Table 5.3). *Amara farcta* also showed a preference for *B. napus* (Indicator Value = 39.2, P = 0.046), while both *A. littoralis* and *Poecilus lucublandus* Say had preferences for *B. rapa* (Indicator Value 61.3, P = 0.015; and Indicator Value 53.3, P = 0.012, respectively).

In 2004, the best fit in the NMS analysis was a two-dimensional plot (stress = 16.383, Monte-Carlo Randomization Test P = 0.039). The coefficients of determination (r^2) of axes 1 and 2 were 0.355 and 0.501 respectively, explaining nearly 86% of the variation in the data. Vectors representing *A. bilineata* communities (0.300) generally pointed toward plots subjected to herbicide treatments (Figure 5.7), especially plots treated at higher rates of sethoxydim. There were significant effects of canola species (T = -4.95, A = 0.067, P < 0.001) and herbicide treatment (T = -1.83, A = 0.058, P = 0.046) on beetle composition (Table 5.2). Indicator Species Analysis determined that *A. bilineata* was strongly associated with the herbicide treatment applied at 100% of the label rate (Indicator Value = 23.8, P = 0.006) and *Amara obesa* Say was associated with herbicide at 10% of the registered application rate (Indicator Value = 35.7, P = 0.019) (Table 5.3). Preferences were shown by *A. bilineata* and *A. littoralis* for *B. rapa* (Indicator Value = 58.1, P = 0.01; Indicator Value = 62.4, P = 0.001, respectively).

Agonum corvus Leconte was also significantly associated with *B. rapa* (Indicator Value 20.8, $P = 0.048$); however, total capture numbers of this species were quite low.

In 2005 the best fit in the NMS analysis was a two-dimensional plot with a stress of 8.265 (Monte-Carlo Randomization Test, $P = 0.0196$). The coefficients of determination (r^2) for the axes were 0.427 and 0.536 respectively, which together explained 96.4% of the variation in the data. Vectors representing *A. bilineata* (0.300) were generally directed away from quadrats with higher weed biomass (0% of the registered herbicide application rate), indicating a preferred association for less weedy habitats (Figure 5.8). The *P. melanarius* vector pointed toward plots of intermediate weed biomass and toward the quadrant characterized by *B. rapa* (Figure 5.8). MRPP analysis did not show any beetle species responses to the herbicide treatment in 2005. However, canola species responses were significant ($T = -5.038$, $A = 0.048$, $P < 0.01$) (Table 5.2). Indicator Species Analysis identified several species that responded to *B. rapa*, including *A. bilineata* (Indicator Value = 65.2, $P = 0.013$), *P. melanarius* (Indicator Value = 57.2, $P = 0.016$), *Notiophilus aquaticus* L. (Indicator Value = 42.3, $P = 0.05$), *A. obesa* (Indicator Value = 20.8, $P = 0.05$), *A. cupreum* (Indicator Value = 63, $P = 0.011$), and *A. quenseli* (Indicator Value = 58.3, $P = 0.05$), while *A. torrida* responded to *B. napus* (Indicator Value = 58.3, $P = 0.016$) (Table 5.3).

5.5 Discussion

This study utilized pitfall trapping for comparing beetle species assemblages and community patterns in the different herbicide treatment plots, a sampling approach selected because it is inexpensive, labor-efficient, and convenient. However, pitfall trap

data can be somewhat deficient because collections can be influenced by various environmental factors and the number and arrangement of the traps (Ericson, 1979; Honêk, 1988; Greenslade, 1964; Niemalä et al., 1986; Raworth and Choi, 2001; Spence and Niemalä, 1994). Nevertheless, the samples reflect activity and density of the beetles (Theile, 1977; Luff, 1982), and the technique does allow collections of beetles in numbers suitable for rigorous statistical analyses (Spence and Niemalä, 1994), which are important considerations because there are no reasonable sampling alternatives for most studies (Kowalski, 1975). Moreover, pitfall traps have proven quite useful as population indices for comparisons of carabid activity between years and across similar habitats (Mitchell, 1963; Niemalä et al., 1990), which were important objectives of this study.

A diverse carabid fauna was observed at the study site (Table A5.1), and it represents some species not previously recorded from central Alberta or western Canada. In addition, it seems that variations in carabid species abundances have occurred over time, possibly in response to changes in agricultural practices or invasions by non-indigenous species and subsequent replacement of indigenous species. For example, *P. melanarius* and *C. fossor* were not listed in Frank (1971) or Doane (1981), yet they are two of the most common species found in this study. Both are invasive alien species of European origin (Lindroth, 1969), and in recent years, *P. melanarius* in particular has come to dominate the carabid fauna in many habitat types (Niemalä et al., 2002; Cárcamo et al., 1995). *Agonum placidum* and *B. rupicola* were relatively common in this study, but Doane (1981) recorded activity densities of both species that were less than one percent of all captures over three years in wheat agroecosystems in Saskatchewan. These species

may be better adapted to canola cropping systems, or may have undergone population expansions over the last 25 years.

Trap captures of the dominant carabid species indicated high activity density levels spanning the entire period of root maggot pre-imaginal activity in canola. In June when most *Delia* spp. oviposition occurs (Dosdall et al., 1994), the carabid fauna was dominated by *P. melanarius*, *B. rupicola*, *A. littoralis*, and *C. fossor*, and throughout July when the majority of the root maggot population is in the larval stages (Griffiths, 1986a), adults of *P. melanarius*, *A. placidum*, and *A. quenseli* dominated the carabid fauna (Figure 5.1). Moreover, *A. littoralis*, *Amara* spp., *Bembidion* spp., and *C. fossor* were shown in previous studies to feed upon *Delia* spp. eggs and larvae (Coaker, 1965; Coaker and Williams, 1963; Finch, 1996; Prasad and Snyder 2004). *Agonum placidum* and *A. littoralis* both reached activity density maxima in early July when root maggot eggs and larvae are common. Finch (1996) reported that every *Agonum* species he tested could consume large numbers of *D. radicum* eggs (range 70 to 118 eggs per beetle per day). Larochelle and Larivière (2003) listed dipterous larvae as a food source for adults of *A. placidum*. Although direct assessments were not made of predation by Carabidae on *Delia* spp., it is evident that there were no phenological impediments to prevent these predators from exploiting this resource, and evidence from the literature suggests that *Delia* spp. likely comprised a component of carabid diets.

In carabids, body size seems to have a role for influencing the effectiveness of different species in root maggot egg predation. Finch (1996) determined the numbers of *D. radicum* eggs consumed by 60 ground beetle species, and observed a linear

relationship between the numbers of eggs consumed and beetle length; a body length of 10 mm seemed to be the upper limit for carabid predators of *D. radicum* eggs.

Prasad and Snyder (2006a, 2006b) found that *P. melanarius*, the most populous contributor to the large beetle population in most years of my study, could lower the activity density of *A. bilineata* and of other small Carabidae, not by reducing actual numbers of individuals, but by decreasing their activity. Predators can reduce prey populations directly through density-mediated interactions or through trait-mediated interactions, such as defensive strategies (Preisser et al., 2005). These interactions should be considered when evaluating responses due to environmental modifications. In a review of how weeds support biological diversity, Marshall et al. (2003) suggested that staphylinid beetles tended to be reduced in activity density captures in weedy situations as a response to competition from Carabidae. Such competitive and interspecific or intraguild interactions could not be measured with the pitfall trapping regime I employed; however, such interactions must be considered as important ecological variables in future community ecosystem studies.

Menalled et al. (1999) found that predation rates of onion fly puparia (*Delia antiqua* Meigen, Diptera: Anthomyiidae) used as model prey items in plots of corn (*Zea mays* L.) were positively correlated with the abundance of carabid beetles. In addition to prey availability, weeds have also been shown to be positively correlated to increases in carabid richness and abundance (Cárcamo et al., 1995; Anderson and Eltum, 2000; Speight and Lawton, 1976). For example, Speight and Lawton (1976) found that combined carabid and staphylinid pitfall trap captures were positively associated with the frequency and abundance of weedy ground cover, but not with vertically growing shoots

of wheat (*T. aestivum*). They also observed a significant positive relationship between the number of *D. radicum* puparia removed and the number of beetles captured. The authors attributed this to a more suitable environment for the beetles, especially to the higher relative humidity found under ground-lying grass shoots. Strategies to manage agroecosystems that increase microhabitat diversity therefore hold considerable promise for enhancing the abundance of carabids and so increasing their effectiveness for reducing pest insect populations.

Crop species was found to influence the abundance and diversity of Carabidae species assemblages in other cropping systems (Cárcamo and Spence, 1994; Butts et al., 2003), and in this study substantial differences were observed between *B. rapa* and *B. napus* in the Indicator Species Analysis. During the three years of this study, most of the statistically significant associations found in the analysis linked beetle species with *B. rapa* (78.6%), and relatively few involved such associations with *B. napus* (21.4%) (Table 5.3). Perhaps the best indicator species were *A. littoralis* and *A. bilineata* that were both captured in significantly higher numbers in *B. rapa* in two of the three years of this study. Such responses suggest an attraction either to the host plant itself, or more likely to indirect characteristics arising from this crop species like microhabitat alteration affecting prey availability, shelter, microclimate, or combinations of these (Landis et al., 2000; Landis et al., 2005).

Activity density of the staphylinid predator-parasitoid, *A. bilineata*, declined with increases in monocotyledonous and dicotyledonous weed biomass in both *B. rapa* and *B. napus* (Figures 5.2, 5.3, 5.6, 5.7, 5.8), and *A. bilineata* was an indicator species for *B. rapa* in 2004 and 2005 (Table 5.3). Similar observations were reported by Dixon et al.

(2004) where *A. bilineata* was captured in rutabaga (*B. napus* var. napobrassica) in higher numbers in bare plots than in plots with rutabaga undersown to clover (*Trifolium repens* L.). Dixon et al. (2004) recorded analogous results from pitfall trap captures of *A. bilineata* and from rearing of *D. radicum* puparia, both of which indicated that the predator-parasitoid was more prevalent in bare plots. These observations of habitat preferences may result from the chemical signals emitted by canola plants and the root maggot hosts of *A. bilineata*. Royer and Boivin (1999) found that *A. bilineata* adults are attracted to volatiles associated with both *D. radicum* and to volatiles produced by its brassicaceous host plants. In plots with low densities of monocotyledonous weeds, volatile signals emitted by canola should be stronger because of reduced interference with weed volatiles, and this could result in greater trap captures of *A. bilineata* in those plots. Neveu et al. (2002) found that when the roots of brassicaceous plants are attacked by *D. radicum*, the plants emit volatiles that attract *Trybliographa rapae* (Westwood), a hymenopteran parasitoid of *D. radicum*. If such volatile compounds exert a similar attraction to *A. bilineata*, it could also explain higher *A. bilineata* populations in plots with low weed densities. Root damage by *Delia* spp. is greater to plants of *B. rapa* than to *B. napus* when grown under analogous conditions (Dosdall et al., 1994; Broatch et al., 2008), and canola grown in association with low densities of weeds is subjected to greater infestations by *Delia* spp. (Dosdall et al., 2003; Broatch et al., 2008). By aggregating where prey and mates are available, *A. bilineata* may minimize energy costs associated with resource foraging.

Manipulating weed biomass through variations in herbicide application rate in canola agroecosystems holds promise for enhancing populations of *Delia* spp. natural

enemies. *Aleochara bilineata* was perhaps the most host-specific natural enemy of root maggots collected in our study. This species demonstrated a preference for plots characterized by low biomass of weeds. It is evident, therefore, that management decisions involving manipulations of weed biodiversity should focus on species-specific responses of the natural enemies and the particular insect pest targeted in the system. In canola cropping systems in central Alberta, where *Delia* spp. are the dominant pest insects, it may therefore not be appropriate to maintain systems with extensive vegetational diversity because this would deter populations of *A. bilineata*. However, maintaining weedy backgrounds could hold greater potential effectiveness when pests like the diamondback moth (*Plutella xylostella* (L.), Lepidoptera: Plutellidae) or bertha armyworm (*Mamestra configurata* Walker, Lepidoptera: Noctuidae) infest canola crops because vegetational heterogeneity could enhance carabid populations and lead to reduced pest infestations if the carabids could successfully attack these lepidopteran larvae.

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Table 5.1: Linear regression estimates for *Aleochara bilineata* activity density as a function of monocotyledonous and dicotyledonous weed dry weights recorded after herbicide application to *Brassica napus* and *Brassica rapa* at Lacombe, AB in 2003 to 2005.

Year	Canola species	Regression estimates[a]			
		a	b	r^2	*P* value
a) monocotyledonous weeds					
2003	*B. rapa*	1.21	-0.14	0.30	0.006
2003	*B. napus*	-	-	-	ns
2004	*B. rapa*	1.99	-0.18	0.25	0.010
2004	*B. napus*	1.91	-0.34	0.35	0.002
2005	*B. rapa*	-	-	-	ns
2005	*B. napus*	-	-	-	ns
combined 2003-2005	*B. rapa*	1.80	-0.36	0.33	<0.001
combined 2003-2005	*B. napus*	1.61	-0.37	0.28	<0.001
combined 2003-2005	*B. rapa and B. napus*	1.70	-0.35	0.28	<0.001
b) dicotyledonous weeds					
2003	*B. rapa*	-	-	-	ns
2003	*B. napus*	-	-	-	ns
2004	*B. rapa*	-	-	-	ns
2004	*B. napus*	-	-	-	ns
2005	*B. rapa*	-	-	-	ns
2005	*B. napus*	-	-	-	ns
combined 2003-2005	*B. rapa*	1.49	-0.28	0.22	<0.001
combined 2003-2005	*B. napus*	1.26	-0.19	0.09	0.012
combined 2003-2005	*B. rapa and B. napus*	1.38	-0.24	0.14	<0.001

[a] Data were fitted to Equation 5.1 (see text). Regression estimates are not presented where results were not significant statistically ($P > 0.05$).

Table 5.2: Multi-Response Permutation Procedure (MRPP) estimates for comparisons between canola species and herbicide application rate for each year of the study.

		MRPP estimates		
Year	Treatment	T	A	P
2003	Canola species	-4.324	0.050	<0.001
	Herbicide rate	—	—	ns
2004	Canola species	-4.95	0.067	<0.001
	Herbicide rate	-1.83	0.058	0.046
2005	Canola species	-5.038	0.048	<0.01
	Herbicide rate	—	—	ns

Table 5.3: Results of Indicator Species Analysis performed to identify associations among species of Coleoptera (Carabidae and the staphylinid, *Aleochara bilineata*) and canola species and herbicide (sethoxydim) treatment for each year of the study. Only those associations are presented where $P \leq 0.05$.

Year	Species of Coleoptera	Canola species or herbicide rate	Indicator species value	*P* value
2003	*Amara farcta*	*B. napus*	39.2	0.046
	Carabus granulatus	*B. napus*	63.8	0.049
	Amara littoralis	*B. rapa*	61.3	0.015
	Poecilus lucublandus	*B. rapa*	53.3	0.012
2004	*Aleochara bilineata*	*B. rapa*	58.1	0.010
	Amara littoralis	*B. rapa*	62.4	0.001
	Agonum corvus	*B. rapa*	20.8	0.048
2005	*Aleochara bilineata*	*B. rapa*	65.2	0.013
	Pterostichus melanarius	*B. rapa*	57.2	0.016
	Notiophilus aquaticus	*B. rapa*	42.3	0.050
	Amara obesa	*B. rapa*	20.8	0.050
	Agonum cupreum	*B. rapa*	63.0	0.011
	Amara quenseli	*B. rapa*	58.3	0.050
	Amara torrida	*B. napus*	58.3	0.016
2004	*Aleochara bilineata*	100% rate	23.8	0.006
	Amara obesa	10% rate	35.7	0.019

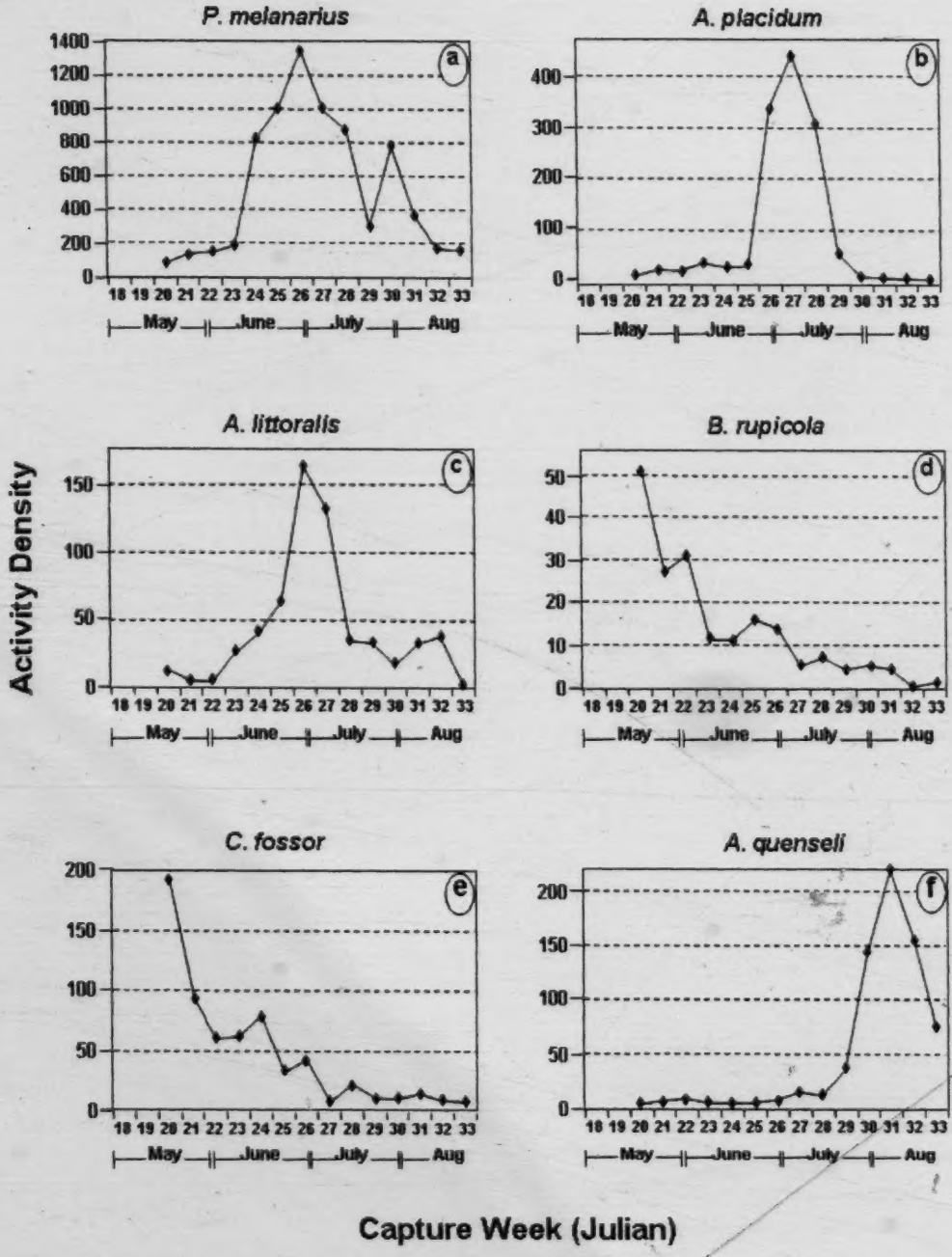

Figure 5.1: Seasonal activity density patterns of Carabidae at Lacombe, AB during 2003 to 2005 combined.

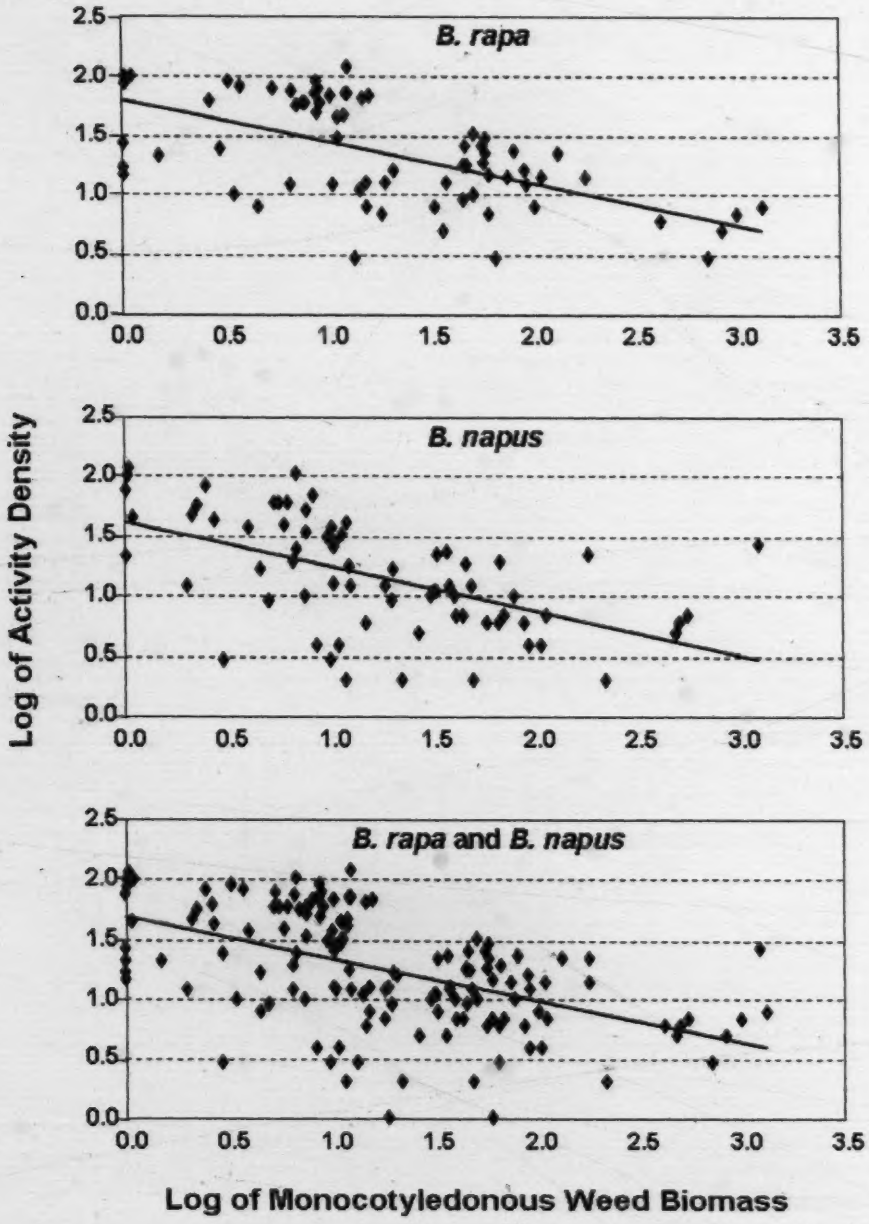

Figure 5.2: Activity density responses of *Aleochara bilineata* Gyllenhal to monocotyledonous weed dry weights in *Brassica rapa*, *Brassica napus*, and both *B. rapa* and *B. napus* at Lacombe during 2003 to 2005. Data were fitted to Equation 5.1 (see text), and curves are based on regression estimates presented in Table 5.1.

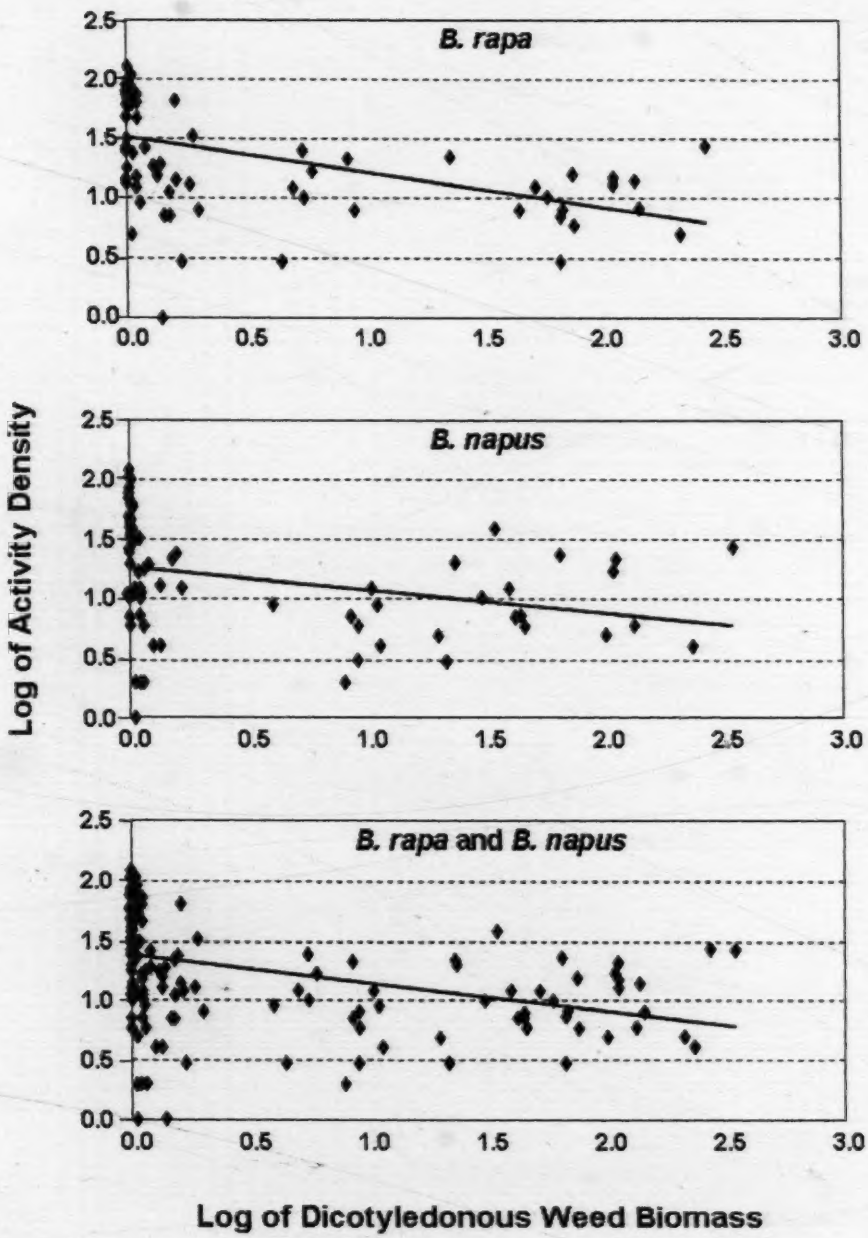

Figure 5.3: Activity density responses of *Aleochara bilineata* Gyllenhal to dicotyledonous weed dry weights in *Brassica rapa*, *Brassica napus*, and both *B. rapa* and *B. napus* at Lacombe during 2003 to 2005. Data were fitted to Equation 5.1 (see text), and lines are based on regression estimates presented in Table 5.1.

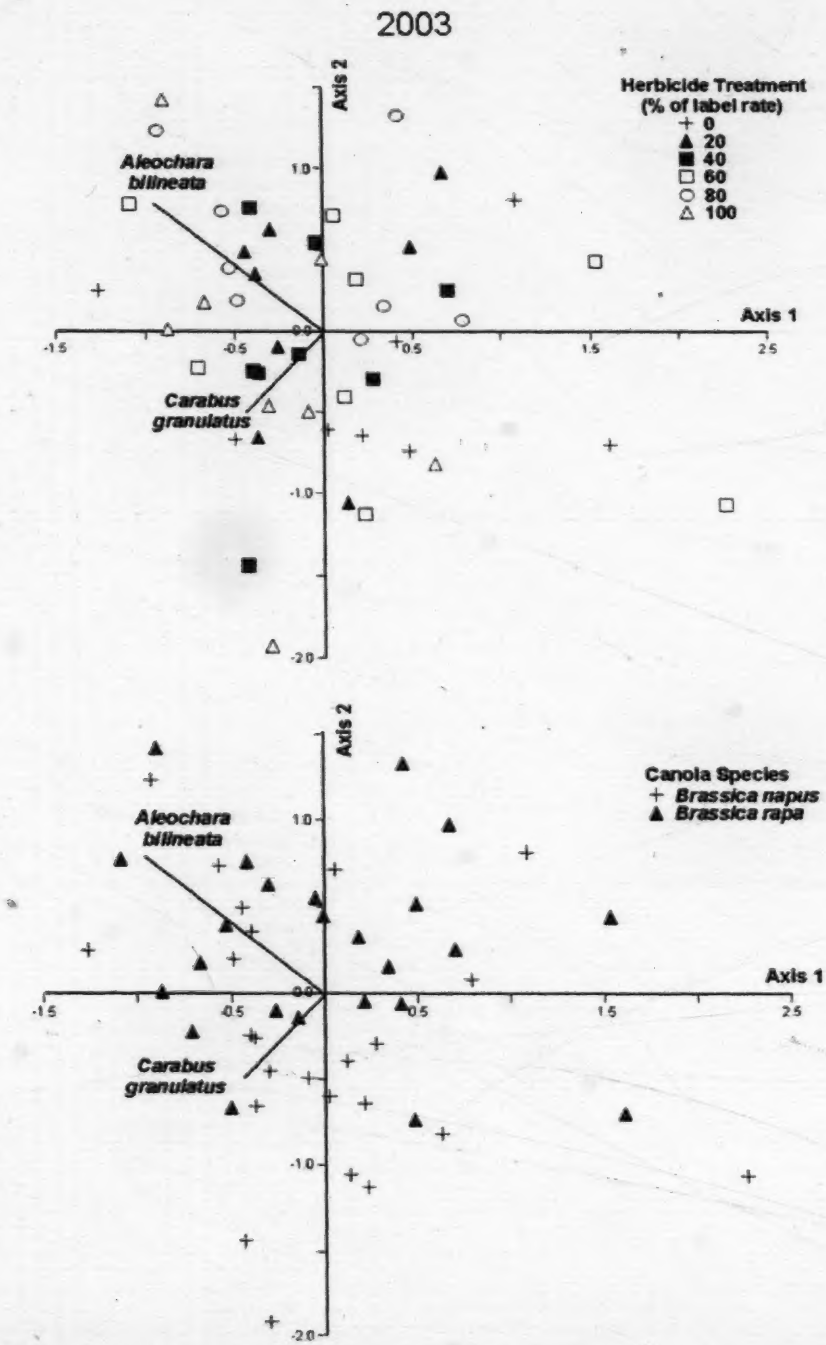

Figure 5.4: Non-metric multidimensional scaling ordination for assemblages of Carabidae and the staphylinid *Aleochara bilineata* captured in plots of *Brassica rapa* and *Brassica napus* subjected to herbicide at different application rates in 2003. Vectors (minimum $r^2 = 0.3$) represent the non-metric multidimensional scaling values for the species identified in the figure.

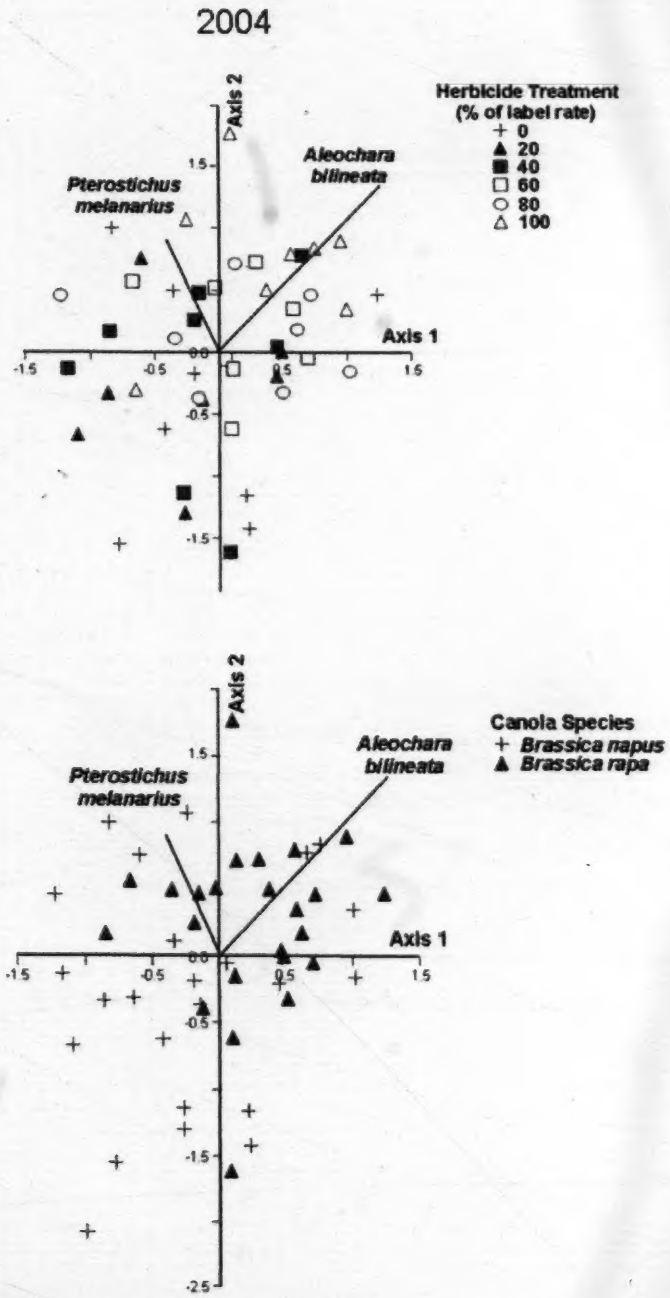

Figure 5.5: Non-metric multidimensional scaling ordination for assemblages of Carabidae and the staphylinid *Aleochara bilineata* captured in plots of *Brassica rapa* and *Brassica napus* subjected to herbicide at different application rates in 2004. Vectors (minimum $r^2 = 0.3$) represent the non-metric multidimensional scaling values for the species identified in the figure.

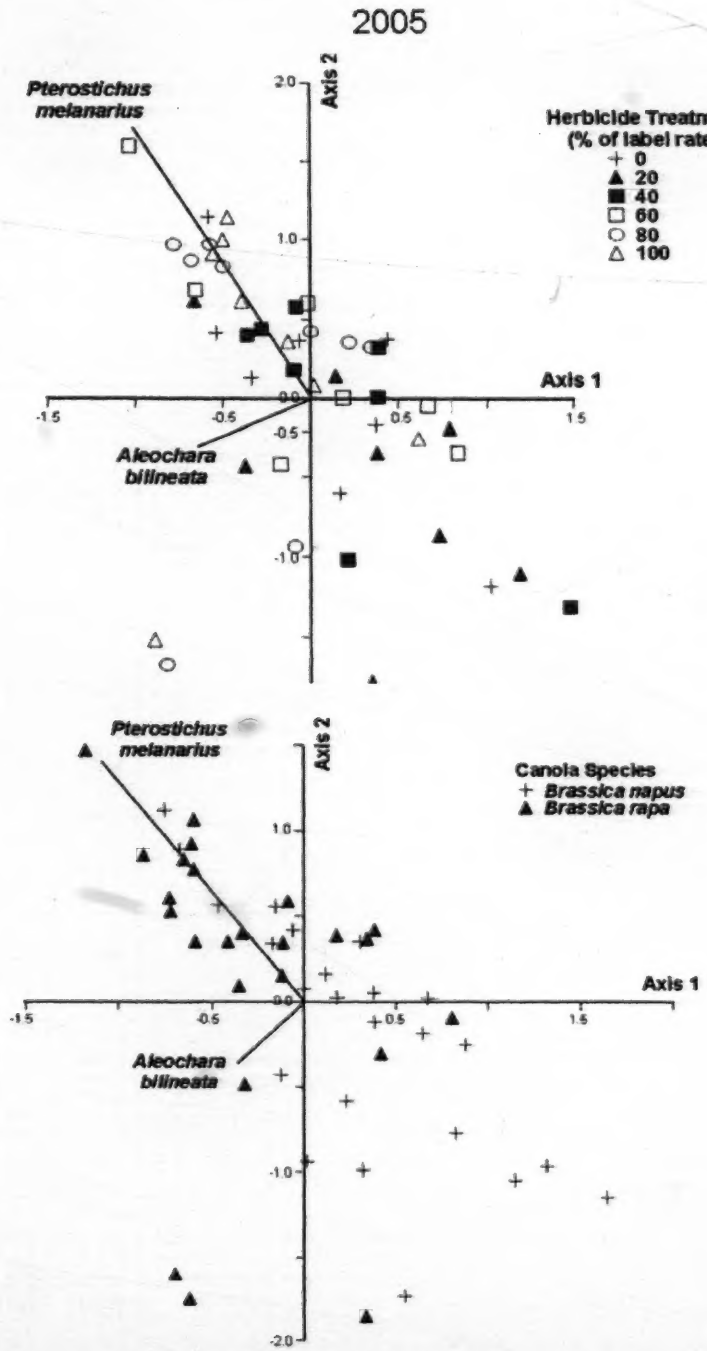

Figure 5.6: Non-metric multidimensional scaling ordination for assemblages of Carabidae and the staphylinid *Aleochara bilineata* captured in plots of *Brassica rapa* and *Brassica napus* subjected to herbicide at different application rates in 2005. Vectors (minimum $r^2 = 0.3$) represent the non-metric multidimensional scaling values for the species identified in the figure.

Appendix: Chapter 5: Responses of Carabid and Staphylinid Species Assemblages to Weed Biomass and Canola Species

A5.1 Background

The research described in Chapter 5 documents some responses of carabid and staphylinid species assemblages to weed biomass and canola species. However, additional data were collected as part of this study and could be important to other researchers in the field of carabid community analysis. The additional data are comprised of regression analysis of beetle body size groups and their responses to weed dry weight measures.

The purpose of this appendix is to present these additional data, and to describe their analyses. The result can therefore provide a more complete representation of the total scope of the study.

A5.2 Materials and Methods

The experimental design and most aspects of agronomic components measured were described in Chapter 5. Here I provide additional descriptions of the method undertaken for this component of the study.

A linear regression analysis was performed using the transformed activity densities of carabids grouped by body size (small: ≤ 5.0 mm, medium: 6.0 – 9.0 mm, large: ≥ 10.0 mm) in relation to the transformed weed density values to investigate the hypothesis that carabids respond differently to weed abundance depending on their body sizes. Log transformed weed dry weight, both monocotyledonous and dicotyledonous,

was used to perform a regression analysis on the catch rate of the carabids grouped by body size using Equation 5.1.

A5.3 Results

In 2003, activity density of small carabid beetles was significantly and positively associated with monocotyledonous weed dry weight in *B. napus* ($y = 0.2933 + 0.1347x$, $r^2 = 0.1909$, $P = 0.03$) (Figure A5.1; Appendix A5.2). In *B. napus*, medium-sized beetles were similarly associated with dicotyledonous weeds ($y = 0.7861 + 0.1958x$, $r^2 = 0.22$, $P = 0.02$), and with total weed populations ($y = 0.6765 + 0.2039x$, $r^2 = 0.2695$, $P = 0.009$) (Figures A5.2; Table A5.2).

In 2004, small beetles were significantly and negatively associated with dicotyledonous weed dry weight in *B. rapa* ($y = 1.0432 - 6.8536x$, $r^2 = 0.1604$, $P = 0.047$) (Figure A5.1), and large beetles were positively associated with dicotyledonous weeds in *B. rapa* ($y = 1.4406 + 6.3976x$, $r^2 = 0.1618$, $P = 0.046$) (Figure A5.2).

In 2005 the only significant effect observed was for medium-sized beetles with dicotyledonous weeds in *B. napus* ($y = 1.3697 + 0.965x$, $r^2 = 0.1748$, $P = 0.04$) (Figures A5.2, Table A5.2).

Overall, responses among small, medium, and large carabid beetles were variable, but in most instances where significant changes were observed, beetle activity density increased as weed biomass also increased.

A5.4 Discussion

I found some significant responses to weed populations by Carabidae of varying body sizes (Table A5.2, Figures A5.1, A5.2). Brust (1990) reported that alteration of habitat did not seem to affect small carabids. However, climate, soil type, moisture, temperature, seasonal period of capture, and weed species would be different in most studies and could have substantial effects on beetle activity density. In this study the most common significant association involved small- and medium-sized beetles, and in four of five instances when statistically significant relationships occurred, activity density increased as weed biomass also increased. These predatory beetles seem to favor environments of greater ecosystem heterogeneity, probably because they provide more diverse microhabitats, allowing for the natural enemies to exploit alternate prey species when their principal prey is not abundant (Altieri and Letourneau, 1984; Landis et al., 2005; Pavuk et al., 1997). Large-bodied beetles increased in *B. rapa* in 2004, in response to increasing dicotyledonous weed biomass (Figure 5.5). This agrees with observations of Bourassa (2006), who captured large carabids with greater frequency as weed density increased. In my study this seemed to occur in a body size group-specific manner: activity density levels of some groups increased more frequently with greater weed biomass, but activity densities of other groups tended to decrease.

Manipulating weed biomass through variations in herbicide application rate in canola agroecosystems holds promise for enhancing populations of *Delia* spp. natural enemies. Several species of Carabidae collected in this study are known to prey upon root maggot eggs and larvae (Wishart et al., 1956; Wright et al., 1960; Pitre, 1965; Ryan and Ryan, 1980), and some species like *P. melanarius* and *A. obsesa* tended to be associated with plots treated with low herbicide rates having greater weed biomass

(Figures 5.4, 5.5, 5.6; Table 5.3). These results corroborate several previous studies that found carabid abundance and biodiversity to increase with greater weed densities in agroecosystems (Cárcamo et al., 1995; Anderson and Eltum, 2000; Speight and Lawton, 1976).

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Table A5.1: Species and frequency of collection (%) of Carabidae in pitfall traps in plots of canola at Lacombe, AB during 2003 to 2005.

Carabid species	2003		2004		2005		Total (2003-2005)	
	No.	Frequency	No.	Frequency	No.	Frequency	Captures	Frequency
Pterostichus melanarius (Illiger, 1798)	85	5.7	1473	32.7	6395	79.6	7953	56.7
Agonum placidum (Say, 1823)	62	4.2	1141	25.3	45	0.6	1248	8.9
Clivina fossor (L., 1758)	23	1.6	382	8.5	355	4.4	760	5.4
Amara torrida (Panzer, 1797)	122	8.2	208	4.6	391	4.9	721	5.1
Amara quenseli (Schonherr, 1806)	134	9	375	8.3	150	1.9	659	4.7
Amara littoralis Mannerheim, 1843	125	8.4	441	9.8	30	0.4	596	4.2
Carabus granulatus L., 1758	305	20.6	1	0	96	1.2	402	2.9
Agonum cupreum Dejean, 1831	41	2.8	35	0.8	219	2.7	295	2.1
Pterostichus adstrictus Eschscholtz, 1823	250	16.9	9	0.2	10	0.1	269	1.9
Bembidion rupicola (Kirby, 1837)	53	3.6	32	0.7	123	1.5	208	1.5
Amara farcta Leconte, 1855	29	2	107	2.4	24	0.3	160	1.1
Poecilus lucublandus (Say, 1823)	38	2.6	72	1.6	12	0.1	122	0.9
Amara lacustris LeConte, 1855	23	1.6	56	1.2	39	0.5	118	0.8
Bembidion quadrimaculatum (L., 1769)	31	2.1	37	0.8	27	0.3	95	0.7
Harpalus amputatus Say, 1830	35	2.4	14	0.3	15	0.2	64	0.5
Notiophilus aquaticus (L., 1758)	28	1.9	13	0.3	34	0.4	75	0.5
Harpalus basilaris (Kirby, 1837)	49	3.3	2	0	6	0.1	57	0.4
Amara apricaria (Paykul, 1790)	0	0	11	0.2	12	0.1	23	0.2
Amara obesa (Say, 1823)	6	0.4	14	0.3	5	0.1	25	0.2
Harpalus affinis (Schrank, 1781)	19	1.3	3	0.1	7	0.1	29	0.2
Amara familiaris (Duftschmid, 1812)	6	0.4	4	0.1	3	0	13	0.1
Bembidion bimaculatum (Kirby, 1837)	2	0.1	5	0.1	7	0.1	14	0.1
Calosoma calidum (Fabricius, 1801)	0	0	7	0.2	3	0	10	0.1
Harpalus fraternus Leconte, 1852	2	0.1	8	0.2	6	0.1	16	0.1

Harpalus fuscipalpis Sturm, 1818	0	0	8	0.2	0	0	8	0.1
Microlestes linearis (Leconte, 1851)	0	0	11	0.2	0	0	11	0.1
Trichocellus cognatus (Gyllenhal, 1827)	3	0.2	6	0.1	0	0	9	0.1
Agonum corvus (Leconte, 1860)	0	0	5	0.1	0	0	5	0
Agonum cupripenne (Say, 1823)	0	0	2	0	0	0	2	0
Agonum propinquum (Gemminger & Harold, 1868)	0	0	1	0	0	0	1	0
Agonum sordens Kirby, 1837	1	0.1	1	0	0	0	2	0
Amara aeneopolita Casey, 1918	0	0	1	0	0	0	1	0
Amara confusa Leconte, 1848	1	0.1	1	0	0	0	2	0
Amara convexa Leconte, 1848	0	0	1	0	0	0	1	0
Amara latior (Kirby, 1837)	0	0	1	0	5	0.1	6	0
Amara pallipes Kirby, 1837	0	0	6	0.1	0	0	6	0
Amara patruelis Dejean, 1831	0	0	1	0	0	0	1	0
Amara scitula Zimmermann, 1832	0	0	1	0	0	0	1	0
Bembidion canadianum Casey, 1924	0	0	0	0	3	0	3	0
Bembidion coloradense Hayward, 1897	0	0	2	0	0	0	2	0
Bembidion nigripes (Kirby, 1837)	0	0	1	0	0	0	1	0
Bembidion nudipenne Lindroth, 1963	0	0	1	0	0	0	1	0
Bembidion obscurellum (Motschulsky, 1845)	0	0	1	0	1	0	2	0
Bembidion obtusangulum Leconte, 1863	1	0.1	0	0	0	0	1	0
Bembidion praecinctum Leconte, 1879	0	0	1	0	0	0	1	0
Bembidion scudderi Leconte, 1878	0	0	0	0	1	0	1	0
Bradycellus congener (Leconte, 1848)	1	0.1	0	0	0	0	1	0
Calathus ingratus Dejean, 1828	0	0	0	0	3	0	3	0
Carabus nemoralis Muller, 1764	1	0.1	0	0	0	0	1	0
Carabus serratus Say, 1823	4	0.3	0	0	0	0	4	0
Chlaenius alternatus Horn, 1871	0	0	0	0	1	0	1	0
Cymindis cribricollis Dejean, 1831	0	0	0	0	2	0	2	0
Diplocheila obtusa (LeConte, 1848)	0	0	2	0	1	0	3	0

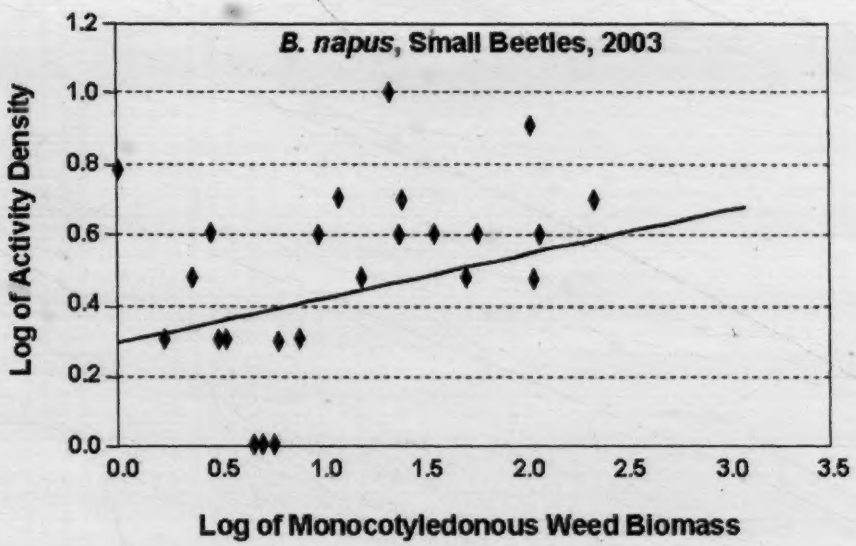
Harpalus somnulentus Dejean, 1829	1	0.1	2	0	0	0	3	0
Patrobus lecontei Chaudoir, 1871	0	0	2	0	1	0	3	0
Patrobus septentrionis Dejean, 1828	0	0	0	0	1	0	1	0
Piosoma setosum Leconte, 1848	0	0	0	0	1	0	1	0
Poecilus corvus (Leconte, 1873)	0	0	1	0	0	0	1	0
Pterostichus riparius (Dejean, 1828)	0	0	0	0	1	0	1	0
	1481	**100**	**4509**	**100**	**8035**	**100**	**14025**	**100**

Table A5.2: Regression estimates for log of the activity densities of small-, medium-, and large-sized adults of Carabidae as a function of log monocotyledonous and dicotyledonous weed dry weights for *Brassica napus* and *Brassica rapa* at Lacombe, AB from 2003 to 2005.

Year	Beetle size	Canola species	Weed type	Regression estimates[a]			
				a	b	r^2	*P*
2003	Small	*B. napus*	Monocot	0.29	0.13	0.19	**0.03**
	Medium			0.95	0.09	0.13	0.09
	Large			1.24	0.01	0.00	0.94
	Small		Dicot	0.53	-0.03	0.00	0.82
	Medium			0.79	0.20	0.22	**0.02**
	Large			1.32	-0.05	0.01	0.68
	Small		Total weed	0.16	0.17	0.12	0.1
	Medium			0.68	0.20	0.27	**0.01**
	Large			1.37	-0.06	0.01	0.59
	Small	*B. rapa*	Monocot	0.60	0.00	0.00	0.92
	Medium			1.19	-0.02	0.01	0.66
	Large			1.11	0.00	0.00	0.96
	Small		Dicot	0.59	0.00	0.00	0.94
	Medium			1.02	0.10	0.11	0.11
	Large			1.01	0.07	0.03	0.42
	Small		Total weed	0.59	0.00	0.00	0.98
	Medium			1.09	0.03	0.02	0.55
	Large			1.04	0.03	0.01	0.67
2004	Small	*B. napus*	Monocot	1.14	-0.15	0.07	0.24
	Medium			1.72	0.02	0.00	0.78
	Large			1.59	-0.19	0.09	0.18
	Small		Dicot	1.03	1.11	0.00	0.82
	Medium			1.73	0.57	0.00	0.80
	Large			1.45	1.05	0.00	0.85
	Small		Total weed	1.14	-0.15	0.07	0.24
	Medium			1.72	0.02	0.00	0.78
	Large			1.59	-0.19	0.09	0.18
	Small	*B. rapa*	Monocot	0.89	0.14	0.08	0.18
	Medium			1.74	2.25	0.05	0.30
	Large			1.57	-0.12	0.06	0.24
	Small		Dicot	1.04	-6.85	0.16	**0.05**
	Medium			1.68	0.10	0.10	0.13
	Large			1.44	6.40	0.16	**0.05**
	Small		Total weed	0.89	0.14	0.08	0.18
	Medium			1.68	0.10	0.10	0.13
	Large			1.57	-0.11	0.06	0.25

Year	Beetle size	Canola species	Weed type	Regression estimates[a]			
				a	b	r^2	*P*
2005	Small	*B. napus*	Monocot	1.38	-0.19	0.12	0.10
	Medium			1.67	-0.15	0.10	0.13
	Large			2.26	-0.14	0.06	0.24
	Small		Dicot	1.06	0.48	0.03	0.40
	Medium			1.37	0.97	0.17	**0.04**
	Large			2.07	-0.49	0.03	0.39
	Small		Total weed	1.38	-0.19	0.12	0.10
	Medium			1.67	-0.15	0.10	0.14
	Large			2.26	-0.14	0.06	0.24
	Small	*B. rapa*	Monocot	0.95	0.06	0.01	0.69
	Medium			1.39	0.04	0.01	0.72
	Large			2.12	0.03	0.00	0.85
	Small		Dicot	1.05	-0.06	0.00	0.88
	Medium			1.47	-0.16	0.01	0.63
	Large			2.14	0.19	0.01	0.62
	Small		Total weed	0.95	0.06	0.01	0.69
	Medium			1.39	0.04	0.01	0.72
	Large			2.12	0.03	0.00	0.85

[a] Data were fitted to Equation 5.1 (see text).



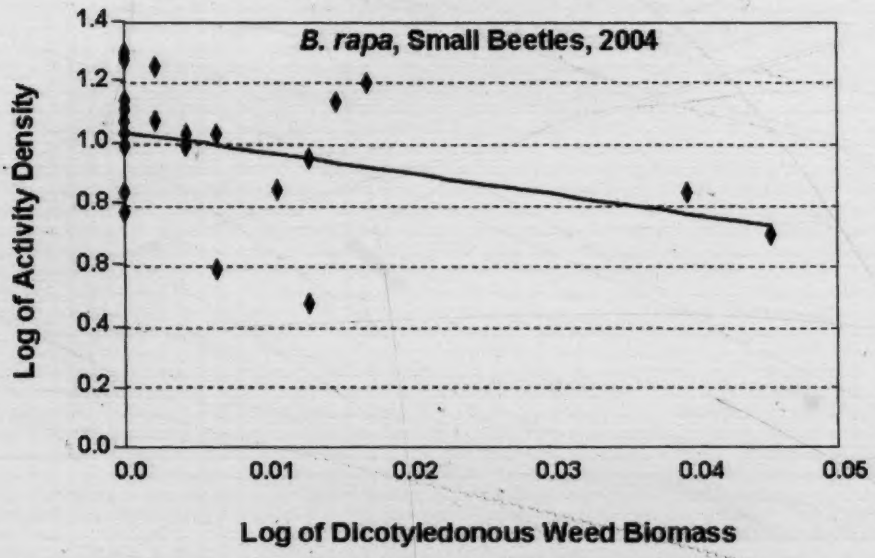


Figure A5.1: Activity density responses of small beetles of Carabidae (≤ 5.0 mm) to monocotyledonous and dicotyledonous weed dry weights in *Brassica napus* and *Brassica rapa* at Lacombe, AB in 2004. Data were fitted to Equation 5.1 (see text), and lines are based on regression estimates presented in Table A5.2.

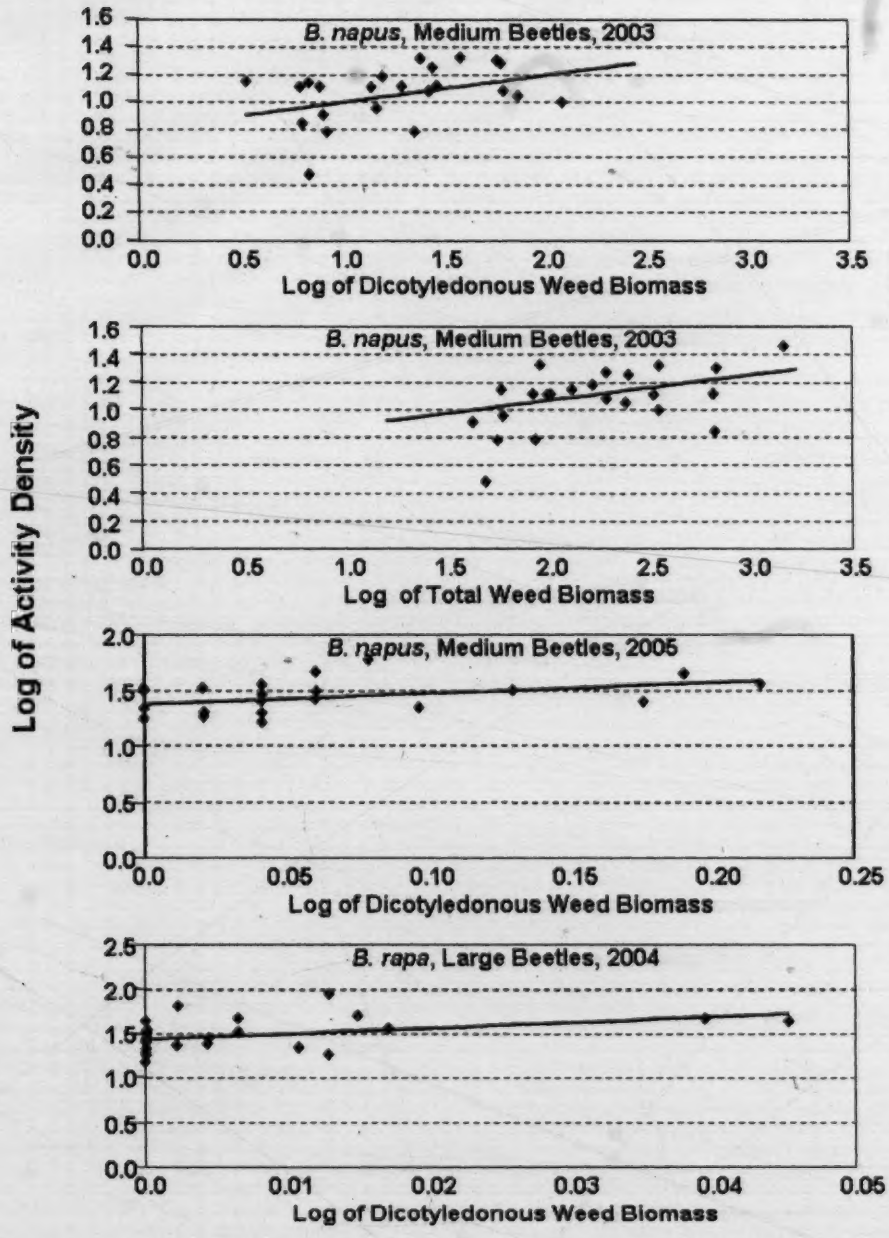

B. napus, Medium Beetles, 2003
Log of Dicotyledonous Weed Biomass
B. napus, Medium Beetles, 2003
Log of Total Weed Biomass
B. napus, Medium Beetles, 2005
Log of Dicotyledonous Weed Biomass
B. rapa, Large Beetles, 2004
Log of Dicotyledonous Weed Biomass
Log of Activity Density

Figure A5.2: Activity density responses of medium (6.0 to 9.0 mm) and large (≥ 10.0 mm) beetles of Carabidae to monocotyledonous and dicotyledonous weed dry weights in *Brassica napus* and *Brassica rapa* at Lacombe, AB in 2004. Data were fitted to Equation 5.1 (see text), and lines are based on regression estimates presented in Table A5.2.

Chapter 6: General Discussion

6.1 Introduction

Over the past 25 years canola (*Brassica napus* L. and *Brassica rapa* L.), grown as an oilseed crop, has become recognized as an important income source and rotational option for producers in western North America. Production in Canada has gradually escalated, so that currently over 5.9 million ha of canola are planted in a wide range of ecosystems (Statistics Canada 2007). This conservatively equates to over three to four billion dollars in revenue annually to the economy of the country. The Canola Council of Canada has released its forecast for canola production for 2015. It is anticipated that canola grown in 2006 on 5.2 million ha in Canada will need to increase by 30% to meet projected market demands (Anonymous, Canola Council website, www.canola-council.org). This is an immense undertaking and will require innovative research on pest management to be successful. Research in western Canada offers an opportunity to gain greater understanding of pest and beneficial organism population structures, and their interactions, in canola agroecosystems. It provides an opportunity to identify agronomic practices and crop conditions that promote beneficial organisms and plant biodiversity to gain advantages in both yield enhancements and environmental sustainability.

A complex of pests attack all above- and below-ground portions of canola crops. Crop losses from insect herbivory can be extremely damaging and are usually most dramatic when outbreak densities develop. Controlling insect pests in canola crops is most commonly achieved through insecticidal applications. Depending on the pest species involved, this can occur as early as planting time in spring with insecticide coated

onto seeds for short-term systemic activity at the seedling stage, or as late as pod-filling stages when foliar insecticide may be applied by aircraft or ground sprayers. Although insecticide applications have provided reliable and reasonably cost-effective control of insect pests in canola, there has recently been greater emphasis placed on minimizing pesticide applications in order to strengthen export markets and ensure greater environmental responsibility. To this end, cultural and biological management strategies have been pursued, and research has been directed toward developing canola varieties resistant to insect infestations. In recent years, there has also been considerable effort to embody integrated insect management within the concept of integrated crop management. This holistic approach is seen as a means of making the most efficient use of energy, various inputs like fertilizers and pesticides, and minimizing environmental impacts to enhance long-term agroecosystem sustainability for profitable production.

Root maggots (Diptera: Anthomyiidae) are key insect pests in canola crops. Several root maggot species occur in canola (Liu and Butts, 1982), but in central Alberta *Delia radicum* (L.) and *Delia platura* (Meigen) are the most common (Broatch et al., 2006). Yield losses in canola due to root maggot attack in central Alberta can range from 20 to 50% (Griffiths, 1991). Dosdall et al. (2003) reported that crop damage to roots and oviposition by females were decreased by 6 and 23% respectively, when weed removal was delayed from the two-leaf to six-leaf stage of canola development. This was believed to be due to an environment where the weeds interfered with egg-laying behavior. However, habitat management for natural enemies and enhanced biological control have also shown some promise. Weeds constitute components of landscape structure and complexity. Many natural enemies of root maggots have been shown to increase in

response to a more heterogeneous environment (Andersen and Eltun, 2000; Cárcamo et al., 1995). Many ground beetles have been reported to feed upon the immature stages of *Delia* spp. (Larochelle and Lariviere, 2003).

An overall goal of my research was to investigate opportunities for enhancing biodiversity of both plants and insects in canola crops as a means of promoting improved integrated crop management and ecosystem sustainability. I studied the influence of weedy backgrounds on the communities of many beneficial insects that affect root maggots in both canola species. I determined the emergence and patterns of seasonal activity of the cabbage maggot, *D. radicum*, the seedcorn maggot, *D. platura*, and the entomophagous rove beetle *Aleochara bilineata* Gyllenhal (Coleoptera: Staphylinidae).

The hypotheses I tested were:

1. H_0: Manipulating weed biomass in canola crops, by reducing rates of herbicide applications, will not influence infestations of root maggots (*Delia* spp.) by lowering damage to taproots in plots having greater weed populations.

H_A: Manipulating weed biomass in canola crops, by reducing rates of herbicide applications, will influence infestations of root maggots (*Delia* spp.) by lowering damage to taproots in plots having greater weed populations.

2. H_0: Manipulating plant biodiversity, by reducing rates of herbicide applications, will not influence beneficial insect populations, specifically predaceous Carabidae.

H_A: Manipulating plant biodiversity, by reducing rates of herbicide applications, will influence beneficial insect populations, specifically predaceous Carabidae.

3. H_0: Manipulating plant biodiversity, by reducing rates of herbicide applications, will not influence *A. bilineata,* the primary predator-parasitoid of root maggot pre-imaginal life stages.

H_A: Manipulating plant biodiversity, by reducing rates of herbicide applications, will influence *A. bilineata*, the primary predator-parasitoid of the root maggot pre-imaginal life stages.

4. H_0: Emergence trap collections made regularly throughout the growing season of newly eclosed individuals of *D. radicum*, *D. platura*, and *A. bilineata* from canola stubble from the preceding year will not enable the development of degree-day predictions of the timing of emergence of these species.

H_A: Emergence trap collections made regularly throughout the growing season of newly eclosed individuals of *D. radicum*, *D. platura*, and *A. bilineata* from canola stubble from the preceding year will enable the development of degree-day predictions of the timing of emergence of these species.

6.2 Thesis Summary

6.2.1 Habitat Enhancement

Habitat management can be used to enhance biological control of insect pests by providing environmental amendments to attract, retain, or increase the effectiveness of natural enemies. Habitat management can also be used to influence the habitats of pests, making these habitats less attractive or detrimental to survival and/or reproductive success. Evaluations of such habitat manipulations are difficult because they often encompass extensive interactions among species and their environment. The difficulties

inherent in investigating and appraising such procedures could deter researchers, because the analyses of such interactions and their interpretations can be tedious and confusing. Habitat diversification or improvement may be influenced by several factors including crop composition, and it stands to reason that the same diversification that enhances natural enemy density and activity could increase or decrease pest populations or pest potential damage. Further, habitat diversification could potentially adversely affect yield, and excessive yield reductions would be unacceptable to growers. Assessments can be especially difficult to evaluate in transitory agroecosystems where crops are rotated annually among different crop species. Nevertheless, important research achievements have been developed within Brassicaceae cropping systems, and have demonstrated success at manipulating pest populations (e.g., Dosdall et al., 1996, 1998; Hellqvist 1996; Humphreys and Mowat 1994; Kostel and Finch 1994; Milbrath et al., 1995; Weiss et al. 1994). A recent review has been published of the impacts of crop diversification in cruciferous crops (Hooks and Johnson 2003), and it is evident that greater effort and attention should be directed toward defining how to utilize non-crop flora, like weeds, in canola cropping systems without prompting significant yield reductions.

In Chapter 3 I presented results of a three-year study conducted during 2003 to 2005 at two sites in Alberta to manipulate monocotyledonous weed populations, and to assess effects on root maggot (*Delia* spp.) populations in canola. Background densities of monocot weeds were varied by altering herbicide applications with rates ranging from 0 to 100% of the rate recommended. This study demonstrated that root maggot damage decreased significantly ($P < 0.01$) with increases in monocotyledonous weed dry weights for both canola species at both study sites. Results support the hypothesis that

heterogenous environments, arising from mixed populations of monocotyledonous weeds within canola, minimized opportunities for females of *Delia* spp. to complete the behavioral sequence required for oviposition, leading to reduced infestation levels in weedy systems. However, effects of dicotyledonous weeds on root maggot infestations varied between sites as a result of site-related differences in weed species compositions. When wild mustard (*Sinapis arvensis* L.) was common, crop damage increased, as this weed can serve as an alternate host for root maggots. Chapter 3 emphasizes the importance of adopting crop management practices that are compatible for both weed and root maggot control.

In addition to the effects of weed biodiversity on root maggot infestations, my studies, summarized in Chapter 5, also determined that weed populations influenced populations of the principal natural enemy of root maggots, the predator-parasitoid, *A. bilineata*, in addition to many species of Carabidae (Coleoptera) inhabiting canola agroecosystems in central Alberta. Data presented in Chapter 5 indicated shifts in the structure and function of predator communities that varied along with differences in crop species and background densities of weeds.

The observations that weedy backgrounds reduced root maggot damage in canola, yet also seemed to reduce *A. bilineata* activity density, seem contradictory. However, my determinations that many carabid populations increased in activity density with a heterogenous background seem to indicate that the overall predator community has a great influence on root maggot egg and larval population regulation. In England, Hughes (1959) calculated that 90 percent of root fly egg mortality was due to predation, and that weather was an important factor affecting predation rates. Consequently, the inclusion of

the entire range of natural enemy species complexes is a necessary requirement for optimal comprehension of those results, and ultimately for exploiting predator-prey relationships for ecosystem management. In the future, studies of community responses to crop management options should be as comprehensive as possible.

6.2.2 Modeling Ecosystems

In some instances cultural and biological control strategies may be at cross-purposes. Habitat modification is likely to affect a broad spectrum of indigenous and recently introduced insects in the community. Biological parameters of herbivores impacted by crop diversification have been related primarily to effects on the specific pests being studied (Hooks and Johnson, 2003). A broad understanding of ecosystem patterns and processes is needed to better evaluate how pests and their natural enemies respond to habitat changes.

In Chapter 2 I determined that the cabbage maggot, *D. radicum*, was univoltine in canola. Peak emergence occurred after approximately 345.8 ± 79.4 degree-days (± S.E.), and 50% flight activity required ca. 324.5 ± 46.8 degree-days (soil base 4°C). *Delia platura* was bivoltine in canola. Peak emergence of the first generation required approximately 339.5 degree-days, and the second generation required ca. 594.5 ± 38.9 degree-days (soil base 3.9°C). Peak flight activity occurred after approximately 255.0 ± 74.2 and 639.9 ± 69.4 degree-days for the first and second generations, respectively. A logistic model, constructed to describe the relationship of degree-days and Julian days with emergence patterns of adult flies, predicted that 10, 50, and 95% emergence of *D. radicum* required 213.7 ± 39.9, 324.5 ± 46.8, and 467.2 ± 46.3 degree-days, respectively.

Logistic analysis predicted that 50% emergence of the first generation of *D. platura* required an average of 255.0 ± 74.2 degree-days, and the second generation required 526.8 ± 66.6, 639.9 ± 69.4, and 952.8 ± 77.0 degree-days for 10, 50 and 95% emergence respectively. Determination of the temporal patterns of abundance of *D. radicum* and *D. platura* has considerable potential for pest management because it can enable growers to time canola seeding to avoid synchronization between host plant growth stages vulnerable to oviposition during peak flight periods of these pests.

My research not only documents the emergence and seasonal activity patterns of these primary pests of canola, but also illustrates that their most important predator-parasitoid can take advantage of the temporal development of root maggots. Temporal synchronization with host populations is critical for survival of a parasitoid population.

In Chapter 4 I reported pitfall trap captures of *A. bilineata* adults within emergence cages situated over canola stubble from the previous year. I determined that approximately 428, 493, and 455 degree-days (soil base 5.57°C) and 187, 189, and 180 Julian days were required for 50% emergence in 2003, 2004, and 2005 respectively (three-year mean = 185.1 ± 2.8 Julian days (S.E.)). Pitfall traps placed in current canola crops determined that 50% levels of activity density required 534, 380, and 559 degree-days and 195, 180, and 186 Julian days, respectively, in each of the three years. A logistic model that described the relationship of degree-days and Julian days with emergence of adult beetles was appraised, and good correspondence was evident between predicted and observed cumulative emergence patterns. Emergence and seasonal activity periods of *A. bilineata* in canola were well synchronized with the occurrence of pre-imaginal life stages of its

principal hosts, *D. radicum* and *D. platura*, with beetle emergence beginning shortly after the onset of root maggot oviposition.

The importance of having two hosts available for *A. bilineata* may be an important consideration when predicting the effectiveness of this natural enemy for regulating host populations. The earlier *D. platura* emergence, relative to *D. radicum*, and existence of a second generation of *D. platura* may provide a more stable system for survival of prey and parasitoids, increasing their overall population stability and reproductive success. A similar circumstance was observed in the onion ecosystem by Carruthers (1981) who found that adding a second host significantly increased the prevalence of the pathogen *Entomophthora muscae* (Cohn) Fresenius (Zygomycetes: Entomophthorales) and its impact on the primary pest population. Earlier emergence of *D. platura* allowed *E. muscae* to reach higher levels earlier in the season, and consequently the pathogen aided more significantly in the control of the onion maggot, *Delia antiqua* (Meigen), in onion crops. We determined that in canola cropping systems of central Alberta, *A. bilineata* does indeed have a good fit with the developmental biologies of both root maggot species, based on the timing of the appearance of egg and larval stages of the dominant pest species, *D. radicum* and *D. platura*. The potential, therefore, exists for the two-host system to provide improved population control overall and enhanced effectiveness of *A. bilineata*, as well as the *E. muscae* pathogen which also occurs in this system.

In Chapter 5 I report that responses among small, medium and large beetles were variable, but in most instances where significant changes were observed, beetle activity density increased with greater plant heterogeneity. Carabid community structure was

influenced by canola species and weed biomass. Significant preferences for canola species were found among several important predaceous beetles. Effects of varying weed populations and canola species on carabid and staphylinid assemblages are complex and require more in-field evaluations and analysis.

These results contribute to an understanding of ecosystem functioning in canola, and to modeling of the canola agroecosystem. Although much more remains to be done, such foundation information can drive future studies to impart greater understanding of multi-trophic relationships and strategies that can be used by producers to manipulate natural enemy populations for improved integrated crop protection.

6.2.3 Indigenous and Exotic Species

Several studies documenting the insect species collected during surveys have shown that the diversity and abundance of carabid species is changing over time (Frank, 1971; Doane, 1981; Spence and Spence, 1988). Large fluctuations in populations of the dominant carabid species, as found in my study, seem to be characteristic of carabid community structure (Butts et al., 2003; Bourassa, 2006). As reported in Chapter 5, in 2003 *Pterostichus melanarius* (Illiger) constituted 5.7% of the carabid population, while in 2005 it constituted 79.6% of the carabid captures. *Agonum placidum* Say is another example of a radical shift in carabid populations; this species comprised 25.3% of the overall carabid population in 2004, versus 4.2% and 0.6% in 2003 and 2005, respectively. Understanding factors influencing these population shifts could be instrumental for devising methods to help stabilize populations of the important predators and so provide more predictable population control of pest insects.

In this study the relative activity densities of both *P. melanarius* and *Clivina fossor* L. were surprisingly high, given their absence from carabid populations in a number of other relatively recent publications (Frank, 1971; Doane, 1981). Both carabids could be important in pest regulation in canola. The relative abundance of *A. placidum*, and the timing of its entry into canola, make it an important component of the natural enemy guild.

The subsequent spread of introduced invasive species, as well as any temporal advantages in densities of indigenous species, would depend on many agronomic influences that might influence those populations, such as plant heterogeneity. Responses could vary widely among species, and new or introduced species may be able to take advantage of host prey if their development is well synchronized with a suitable host or food source. Similarly, indigenous species can adapt or expand their abundance levels and distributions to exploit new or expanding opportunities. In western Canada, canola is grown in vast areas of cropland and *D. radicum* and *D. platura* provide an enormous food resource, which opportunistic, generalist carabid species can continue to exploit. My study is the first of its kind to describe the species composition and community structure of beetle predators and parasitoids in canola, and it can be used as a basis of comparison of how these ecosystems change over time.

6.2.4 Climate Change

Predators, and especially parasitoids, depend on the temporal activity patterns of their hosts, and so are highly susceptible to changes in the environment. An emerging focus of research in insect-host plant interactions relates to possible disruptions that can

occur with impending climate change in the synchronization of herbivorous hosts and their natural enemies. Hosts and parasitoids may have different thermal preferences or different capacities to survive extreme temperatures (Hance et al., 2007). Climate change can lead to restructuring of arthropod communities, and influence the adaptation of parasitoids to new or previously available host species. The importance of having *D. platura* in the canola ecosystem is representative of such a situation. *Aleochara bilineata* populations will likely be more temporally responsive to root maggot populations in general when a dual host is available, and the multivoltine habit of *D. platura* can perhaps ensure that hosts are available for *A. bilineata*. In the future, this synchrony may be of great importance in the ability of *A. bilineata* to regulate root maggot populations. Each root maggot species, as well as its parasitoids, can be affected by such changes and may or may not be able to adapt. Changes in fecundity, longevity, mobility and ability to orientate to attractive odors can be affected by temperature (Hance et al., 2007), and effects of such broad ecosystem alterations are difficult to predict.

Temperature is the dominant abiotic factor directly affecting herbivorous insects and it directly affects insect development, survival, range and abundance (Bale et al., 2002). Consequently, temperature can affect insect overwintering success, and is predicted to impact the range and abundances of various pest species. Expansion of range is predicted for populations of the grasshopper *Melanoplus sanguinipes* (F.) (Orthoptera: Acrididae) in Canada if temperatures rise even between 1 to 7°C (Olfert and Weiss, 2006a). The invasive alien species *Oulema melanopus* L. (Coleoptera: Chrysomelidae), *Meligethes viridescens* (F.) (Coleoptera: Nitidulidae) and *Ceutorhrynchus obstrictus* (Marsham) (Coleoptera: Curculionidae), recently introduced

to Canada, will likely experience increased ranges and abundance levels according to even conservative climate change scenarios (Olfert and Weiss, 2006b). The ability of pests to overwinter in western Canada may also complicate the interactions and successfulness of parasitoids for regulating host populations, as well as the choices of control products used if the populations migrate great distances, as in *Plutella xylostella* (L.) (Dosdall, 1994; Dosdall et al., 2004).

Generalist predators are important in ecosystem management because pest species abundances can vary dramatically from year to year, and these predators can expand their host ranges to accommodate such changes. Floate et al. (1990) reported *A. placidum* and *Bembidion rupicola* Kirby (Carabidae) as two of the most common and efficient carabids in the natural control of the wheat midge, *Sitodiplosis mosellana* (Gehin) (Diptera: Cecidomyiidae), in wheat in Saskatchewan. In my study these species were among the most common carabid species present in canola, and in combination with *A. bilineata* seem to serve as an important natural enemy of root maggot pre-imaginal life stages. Having multiple host options will benefit many generalist predator populations. In the future, understanding these tritrophic relationships should become increasingly important, both for biological control and for improving climate modeling scenarios.

I have reported the temporal dynamics for two root maggot species, one predator-parasitoid and selected generalist predator species, but much more research remains to be done on the species network comprising this system. Future research may enable prediction of how climate change can impact community structure and function in our agroecosystems, but most insect pests of new and emerging crops have not been studied in depth, at least not to the extent of understanding their temporal and degree-day

synchronizations within our ephemeral cropping systems. Future research needs to consider insect herbivore phenotypic and genotypic flexibility, the herbivore and natural enemy responses to global climate change parameters, and awareness that some climate change impacts may only become apparent in the longer term.

6.3 Implications to Agricultural Decision Making and Farming Practices

6.3.1 Methods of collection and interpretation: Inclusive methods

Predator effectiveness is dependent on many factors, including their temporal synchrony and thus ability to exploit or colonize their host(s). Daily activity patterns, based on temperatures or microclimates within the crop, can also affect their success (Raworth and Choi, 2001). More effort should be expended to determine how intercrops or mixed cropping systems impact population dynamics and success of natural enemies.

Improved management of canola agroecosystems will be reliant upon adopting the most appropriate agronomic options that can be readily implemented by producers. Attempts should be made to exploit options that provide the most sustainable means of pest control. Evaluation of appropriate options should include determinations of sublethal effects on beneficial organisms (Desneux et al., 2007). In Europe, efforts are underway to develop a standard approach to nontarget assessments when pesticides are used (termed the European Standard Characteristics of Nontarget Arthropod Regulatory Testing ESCORT2) to develop a method to improve the risk assessment of pesticides on natural enemies and propose the adoption of a hazard quotient (HQ) approach (Desneux et al., 2007). The HQ is calculated using a lethal rate of 50, found in laboratory studies, using two sensitive indicator species. This method should give producers an additional

way to calculate economic thresholds that could include the value of beneficial insects in their decision-making processes. Growers in organic production systems and others who wish to minimize the use or expense of traditional pesticides should also benefit from the HQ approach.

Cruciferous plants, in general, do not compete well with background vegetation (Bell, 1995; Bottenberg et al., 1997; O'Donovan et al., 1988; O'Donovan, 1991); however, several strategies could be employed to ecosystem management to accommodate this effect. Early planting of canola to avoid competition from weeds would result in a less competitive background challenge (O'Donovan, 1992, O'Donovan et al., 2007), and should be included in economic threshold calculators. Using vigorous and rapidly growing canola cultivars could be employed to overcome yield losses due to competition, and will soon be available for improving the accuracy of these calculations.

Management of within-field species diversity (flora and fauna) could be used to influence predator numbers and predation rates. In current agricultural production systems, motivation to enhance natural control is based primarily on environmental arguments. In most cases the practical aim is to reduce insecticide applications and their associated costs and health-related concerns. Future support will need to come from technological and socioeconomic arenas, in that researchers should consider beneficial insects and the ecosystem impacts when assessing control options, and consumers will need to support production systems that involve potential increases in cost of produce. Producers will need to see a monetary or environmental benefit to adopting new strategies.

6.4 Conclusions, Future Research and Recommendations

6.4.1 Conclusions

- *Delia radicum* and *D. platura* are the dominant root maggot species in canola agroecosystems in central Alberta.
- *Delia radicum* is univoltine in canola and peak emergence occurred after approximately 345.8 ± 79.4 degree-days (± S.E.), and 50% flight activity required approximately 324.5 ± 46.8 degree-days (soil base 4.0°C).
- *Delia platura* is bivoltine in canola and peak emergence of the first generation required approximately 339.5 degree-days (soil base 3.9°C), and the second generation required approximately 594.5 ± 38.9 degree-days (soil base 3.9°C). Peak flight activity occurred after approximately 255.0 ± 74.2 and 639.9 ± 69.4 degree-days for the first and second generations, respectively.
- Root maggot damage decreased significantly ($P < 0.01$) with increases in monocotyledonous weed dry weights for both canola species.
- Effects of dicotyledonous weeds on root maggot infestations varied between sites as a result of site-related differences in weed species complexes.
- Collections of *A. bilineata* adults within emergence cages situated over canola stubble from the previous year indicated that approximately 428, 493, and 455 degree-days (soil base 5.57°C) and 187, 189, and180 Julian days were required for 50% emergence in 2003, 2004, and 2005 respectively (three-year mean = 185.1 ± 2.8 Julian days (S.E.)).

- Pitfall traps placed in current canola crops determined that 50% levels of activity density for *A. bilineata* required 534, 380, and 559 degree-days and 195, 180, and 186 Julian days, respectively, in each of the three years.
- *Aleochara bilineata* populations in canola were well synchronized with occurrence of pre-imaginal life stages of its principal hosts, *D. radicum* and *D. platura*, with beetle emergence beginning shortly after the onset of root maggot oviposition.
- As weed biomass declined, the activity density of the root maggot predator-parasitoid *A. bilineata* increased ($P < 0.01$).
- Overall beetle community structure was influenced by weed biomass. Responses among small, medium, and large carabid beetles were variable, but in most instances where significant changes were observed, beetle activity density increased as weed biomass increased.
- Overall beetle community structure was influenced by canola species. Significant preferences for canola species were found among several important predaceous carabid beetle species, including the carabids *Amara littoralis* Mannerheim, *Amara farcta* Leconte, and *P. melanarius*, and the staphylinid *A. bilineata*.

Fundamental knowledge directed at determining how both pest and beneficial insect species interact within canola agroecosystems is still very limited, and developing such knowledge necessitates investigation and documentation across a series of ecoregions in western Canada. Additional information on the taxonomy, ecology and distribution of the different species is required before evaluations of cropping practices

can be more fully understood. Assessments made in Europe, for example, may not necessarily be applicable to our northern climate and ephemeral cropping systems. How these insects interact in response to cropping adjustments is currently based to a large degree on mostly conjectural or anecdotal evidence. Yet, in order to make recommendations to canola producers, such cropping adjustments need to be objectively validated and predictable. Influences such as soil type, tillage system, microhabitat, field flora, temporal development, and many agronomic options could affect the complexity and magnitude of these interactions. By studying selected sample sites in detail, a reference point could be developed for ecological analysis and long-term monitoring data.

6.4.2 Future research and Recommendations

Both pest and beneficial insect populations can fluctuate extensively from year to year in canola production systems, and the mechanisms that determine this needs to be investigated. Interactions between pest species and beneficial insects can be documented, but the relationship of environment, crop type, and agronomic practices to these interactions have yet to be described. Models for weed decision-making processes are beginning to be developed and will eventually become available to producers. Similar frameworks, incorporating previous studies of pest-beneficial interactions and meteorological records, need to be incorporated into technical spray decision guidelines.

Managers of agroecosystems should become more aware of the structure and processes that regulate biological cycles within these systems, so that we can identify opportunities to modify and enhance these interactions for enhanced ecosystem

sustainability. A more comprehensive understanding of host, predator, parasitoid and crop dynamics will allow us to utilize these systems more effectively as components of multifaceted pest management planning.

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